

THE OSTRACODERM *PHIALASPIS* FROM THE LOWER DEVONIAN OF THE WELSH BORDERLAND AND SOUTH WALES

by P. R. TARRANT

ABSTRACT. The Lower Devonian ostracoderm *Phialaspis symondsi* differs sufficiently from the type species of the Traquairaspididae, *Traquairaspis campbelli*, to place it within a separate family, the Phialaspididae. This family also includes *Toombsaspis pococki* comb. nov., *T. sabrinae* comb. nov. and *Munchoaspis denisoni* comb. nov. The Traquairaspididae includes *Traquairaspis campbelli* and *Rimasventeraspis angusta* comb. nov. A new reconstruction of the carapace of *Phialaspis symondsi* is given and, from an examination of immature plates, a possible mode of growth is outlined. Likely feeding and respiratory mechanisms are discussed. A new form of jet-aided steering is proposed for phialaspidid ostracoderms.

The inner surface of a heterostracan ventral median plate was described by Lankester (1868) as *Cyathaspis symondsi*. Later Traquair (1898) described plates with a stellate tubercular ornament as *Psanmosteus anglicus*, from which the *Psanmosteus* Limestone is named. Wills (1935) and White (1946) described the morphology of the carapace under the name *Phialaspis* combining Lankester's and Traquair's material (transferred to *Traquairaspis* in 1948 by White and Toombs). More recently, Dineley and Loeffler (1976) have added to the knowledge of general traquairaspidid morphology by their descriptions of Canadian material with dorsal shields formed of fused plates.

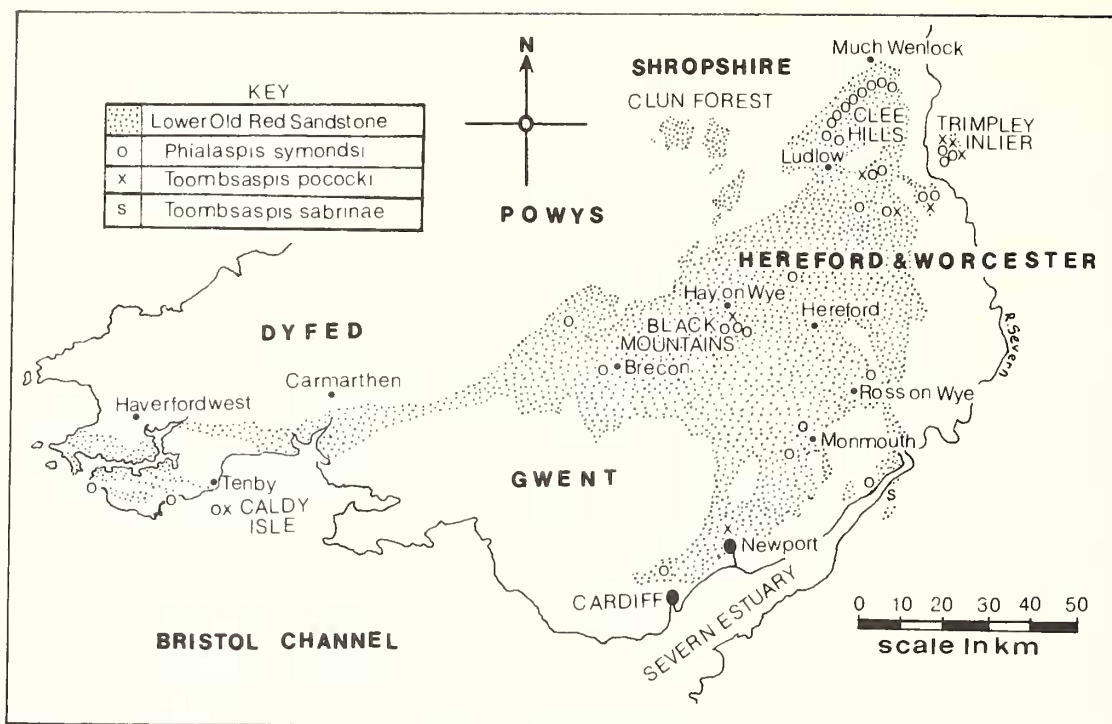
The bulk of the *Phialaspis symondsi* material described in this work (over 200 specimens) came from Devil's Hole stream section (also known as the Lye Brook: White and Toombs 1948; White 1950*b*; Ball and Dineley 1961) which dissects the Lower Devonian, Downton/Ditton Group transition (White 1950*a*) of the Lower Old Red Sandstone, Morville district, Shropshire. This is mainly the result of sixteen years of collecting by Mr A. M. Tarrant and the author. Also included, are descriptions of specimens collected from the site by the late Mr H. A. Toombs and Professor D. L. Dineley, and material collected to be studied as part of a palaeoecological project when the Nature Conservancy excavated the site in 1981. Material of *Phialaspis symondsi* and *Toombsaspis pococki* collected from elsewhere within the Anglo-Welsh Region (Text-fig. 1) and the Scottish *Traquairaspis campbelli* was also studied.

ANGLO-WELSH LOCALITIES

Details of localities 2–4 and 6–14 are listed in Ball and Dineley (1961). Further information on all the localities given below is deposited with the Nature Conservancy Council, Geological Review Unit, Peterborough, to which enquiries may be directed.

Shropshire (Clee Hills District): (1) Barnsland Farm Quarry; (2) Clapgate Quarry; (3) Devil's Hole; (4) Earnstrey Brook; (5) Gardener's Bank; (6) Great Oxenbold Stream; (7) Hudwick Dingle; (8) Kidnall Gutter; (9) Little Oxenbold; (10) New Buildings; (11) New Inn; (12) Oak Dingle; (13) Sudford Dingle; (14) Targrove Quarry. *Phialaspis symondsi* is found at all these localities, with *Toombsaspis pococki* found in addition in a separate horizon at locality 5.

Hereford and Worcester: (15) Birch Hill Quarry, The Trimpey Inlier; (16) Cradley Quarries, The Trimpey Inlier; (17) Common Bach, Dorstone, Black Mountain District; (18) Cusop Dingle, Black



TEXT-FIG. 1. Known phialaspidid localities in the Anglo-Welsh Lower Old Red Sandstone, indicated by symbols as shown in the key.

Mountain District; (19) Eastham Brook, The Trimpley Inlier; (20) Heath Farm, Wolferlow, The Trimpley Inlier; (21) Holbeach House Stream, The Trimpley Inlier; (22) House of the Wood Quarry, Garnon's Hill, Heightington; (23) Hurtlehill Farm Quarry, Heightington; (24) Llan Farm, Dorstone, Black Mountain District; (25) Man Brook, The Trimpley Inlier; (26) Mary Moors, The Trimpley Inlier; (27) Merbach Brook, Ledbury; (28) Park Atwood Stream, The Trimpley Inlier; (29) Ross Motorway, M50 section; (30) Sapey Brook, Thrift Farm; (31) Shatterford, Boundry Brook, The Trimpley Inlier; (32) Westhope Hill, near Hereford; (33) Witchery Hole, Clifton on Teme. *Phialaspis symondsi* found at all localities except 28 and 31, at which *Toombsaspis pococki* was found. Both species present at localities 18 and 33, in the same horizon only at the latter.

Powys: (34) Onen, Court Wood Quarries; (35) Pen-y-lan, Crwews Wood Quarries. *Phialaspis symondsi* found at both localities.

Gwent: (36) Alteryen Quarry, *Toombsaspis pococki*; (37) Coed-y-coedcae, *Phialaspis symondsi*; (38) Penrhos Farm Quarry, *Phialaspis symondsi*.

Gloucestershire: (39) Lydney, *Phialaspis symondsi*; (40) Sharpness Docks, *Toombsaspis sabrinae*.

Dyfed: (41) Caldy Island, *Phialaspis symondsi*, *Toombsaspis pococki* (several horizons); (42) Freshwater West, *Phialaspis symondsi*; (43) Manorbier Bay, *Phialaspis symondsi*.

MATERIALS AND METHODS

To obtain information about their outer surfaces, the Toombs and Rixon (1950) transfer method was used on several specimens. This entailed mounting the specimens on clear resin, and removing the matrix with acetic acid. Although several specimens prepared reasonably well, the results were mixed. The larger plates had a tendency to be destroyed by the acid owing to the calcite infill of their cancellous spaces. A limited amount of success in tracing the sensory canal system came from impregnating certain specimens with oil of aniseed and viewing them in transmitted light. Often it was necessary to remove the aspidin with dilute hydrochloric acid (White 1935, 1946). Many specimens were not prepared because of the risk of damage to their inner surfaces.

The bulk of material is new and is housed in Ludlow Museum, Shropshire, SHRCM.G – 235 specimens, and in the National Museum of Wales, Cardiff, NMW – 6 specimens. Other specimens studied are from established collections housed in the following museums: British Geological Survey Museum, Kegworth, Notts., BGS (GSM); British Museum (Natural History), London, BMNH; University of Birmingham Geology Museum, BU; National Museum of Canada, Ottawa, NMC; Princeton University Geological Museum, New Jersey, USA, PU; Royal Museum of Scotland, Edinburgh, RSM; W. F. Whittard collection, S.

STRATIGRAPHY AND PALAEOECOLOGY

Most of the heterostracans described in this work came from the Upper Downton Group, Lower Old Red Sandstone, Anglo-Welsh Region. The stratigraphy and sedimentology of this area have been documented by Ball and Dineley (1961); Allen and Tarlo (1963); Allen (1964, 1974*a*, 1974*b*, 1985); and Allen and Williams (1978, 1981). It is dominated by red mudstones, which are interspersed with discrete beds of upwardly fining, current-influenced units of sandstones and intraformational conglomerates. The conglomerates usually hold the largest concentrations of vertebrate fossils.

Most recent workers in the field have considered that they represent infilled freshwater channel complexes, within an extensive deltaic floodplain (Ball and Dineley 1961; Allen and Tarlo 1963; Allen 1964, 1974*a*, 1974*b*).

The area is dissected by the *Psammosteus* Limestone, a pedogenic feature (see Allen 1974*a*, 1985), which divides the Downton from the overlying Ditton. Although rare specimens of *Phialaspis symondsi* have been found above the *Psammosteus* Limestone, this horizon marks a distinctive faunal change, where the phialaspids are replaced by pteraspidiforms (White 1950*a*; Ball and Dineley 1961).

White (1950*a*) used *Phialaspis symondsi* as a zone fossil marking the uppermost Downton, and *Toombsaspis pococki* to mark the underlying zone. The base of the range of *Phialaspis symondsi* is about 30 m below the *Psammosteus* Limestone. Recent field studies (Rowlands and Tarrant, unpublished data), would suggest that the top of its range is considerably less than Ball and Dineley's (1961) claim of *c.* 53 m above the *Psammosteus* Limestone. The bulk of *Toombsaspis pococki* material studied by White (1946), came from 5 m below the *Psammosteus* Limestone at Gardener's Bank, Shropshire, which is the top of its range. Squirrel and Downing (1969) collected fragments which they considered to belong to this species from 158 m below the *Psammosteus* Limestone at Ateryn Quarry, Gwent, which may be the bottom of its range. However, it would appear that the two species substantially overlapped in time.

They have only been recorded together at the Witchery Hole, Clifton on Teme, Hereford and Worcester (Ball and Dineley 1961), where the material was in loose blocks and may have originated from different horizons (M. A. Rowlands, pers. comm.). As Ball and Dineley suggested, this could indicate that they occupied different environments. Following this, the two species are mainly found with different vertebrate faunas. *Phialaspis symondsi* is characteristically found with *Tesseraspis tessellata*, *Anglaspis macculoughi*, *Corvaspis kingi*, *Turinia pagei*, cephalaspids, *Ischnacanthus wickhami* and other acanthodians (Ball and Dineley 1961; Turner 1973). It is also occasionally

found with *Protopteraspis gosseleti*, *Pteraspis rostrata* and *Nodonchius* sp. *Toombsaspis pococki* is associated with *Tesseraspis tessellata*, *Didymaspis grindrodi* and other cephalaspids, the *Goniporus-Katoporus* thelodont fauna, *Ischnacanthus kingi* and other acanthodians (White 1946; Turner 1973).

It would seem that the overlapping vertebrate assemblages of the horizons subjacent to the *Psammosteus* Limestone are related as much to varying ecological conditions as they are to time. Indeed, Karatajute-Timalaa (1978) and Blicek (1984) proposed that the zones of *Traquairaspis symondsi* and *Traquairaspis pococki* should be amalgamated into a single *Traquairaspis* zone. However, because of the reclassification of these species in this work, it is proposed that it should be renamed the *Phialaspis symondsi-Toombsaspis pococki* zone.

As Ball and Dineley (1961) observed, the vertebrate remains are often fragmented, and concentrated in pockets with individual specimens of a similar size, buoyancy, or weight, suggesting that they were probably originally transported, water selected, and in some cases may have been reworked. Their preservation is usually good, often showing fine details, and the vascular cancellous layers are normally not crushed, because of calcite infilling.

SYSTEMATIC PALAEONTOLOGY

Subclass HETEROSTRACI Lankester, 1868

Order TRAQUAIRASPIDIFORME Tarlo, 1962

Diagnosis. (After Dineley and Loeffler 1976). Dorsal shield comprises either single plate or single dorsal disc, rostral and pineal plates, and paired orbital, branchio-cornual or branchial and cornual plates. Orbital, pineal and branchial openings enclosed. Ornamentation of dorsal shield often of elevated, laterally serrated tubercles, commonly with narrow interstitial tubercles or ridges, mainly arranged in cyclomoriform units, sometimes with outer adult plate growth. Ventral disc ovate to elongate, with lateral ornamentation similar to dorsal shield, becomes broader and flatter towards longitudinal midline, or replaced by smooth, flat, ovate central area. Lateral line system variable, ranging from pattern of longitudinal canals and transverse commissures to anastomosing network.

Discussion. Although *Weigeltaspis* may prove to be a traquairaspidiform (Obruchev 1964; Blicek 1983), this has yet to be established. It is possible that the Canadian *Traquairaspis* and *Nataspis* Dineley and Loeffler, 1976, with ornamented ventral central regions, may prove to represent different evolutionary lineages from those species with smooth ventral central regions.

White (1950a) realised that the specimens he had described as *Phialaspis pococki* subsp. *cowiensis* White, 1946 were ventral discs of *Traquairaspis campbelli*, and he reclassified *Phialaspis pococki* and *Phialaspis symondsi* as members of the genus *Traquairaspis*. However, following Halstead's (1982) retention of the name *Phialaspis*, the British species can be divided into two distinct morphological groups. They are considered in this work to represent two distinct families, the Traquairaspididae and the Phialaspididae.

Family PHIALASPIDIDAE White, 1946

Type genus. *Phialaspis* Wills, 1935

Other genera assigned. *Toombsaspis* gen. nov., *Munchoaspis* gen. nov.

Diagnosis. Dorsal shield usually comprises seven separate plates. Dorsal disc quadrate, vaulted posteriorly, with median row of large cyclomoriform units on posterior half forming a keel, and usually a dorsal vane. Ventral disc flattening and widening anteriorly with raised, smooth, coffin-shaped central area, situated more posteriorly than anteriorly and enclosed by ornamented margin of disc. Two rows of longitudinally running, large cyclomoriform units on each lateral side of dorsal disc, one row on each lateral side of ventral disc, another row on dorsal side of each branchio-

cornual plate. Regions of cyclomoriform adult growth on anterior and lateral edges of dorsal and ventral discs. Paired lateral plates, with, quite frequently, separate paired post oral plates.

Genus PHIALASPIS Wills, 1935

Type species. Cyathaspis (?) symondsi Lankester, 1868

Diagnosis. Large advanced Phialaspididae. Dorsal discs more vaulted than ventral disc. Dorsal vane large with two cyclomoriform units, median keel with one. Rostrum enlarged. Branchio-cornual plates with lateral keels terminating posteriorly in lateral vanes. Ventral disc with non-unital cyclomoriform growth between longitudinal units and smooth central region, with three units positioned behind and sometimes fused to its posterior edge. Ornament of stellated tubercles, which are often ringed on the reticular layer by a groove or shelf.

Phialaspis symondsi (Lankester, 1868)

Plates 1-4; Plate 5, figs 2-5; Plate 6; Text-figs 1-10, 13, 14A,B, 15A-G, 16; Table 1

1868 *Cyathaspis (?) symondsi* Lankester, p. 27, pl. 6, fig. 5.

1898 *Psammosteus anglicus* Traquair, p. 67, pl. 1, figs 1 and 2.

1935 *Phialaspis symondsi* (Lankester); Wills, pp. 439-444, pls 5-7; text-fig. 4.

1948 *Traquairaspis symondsi* (Lankester); White and Toombs, p. 7.

Holotype. BGS(GSM)31380, ventral disc.

Horizon and localities. Upper Silurian/Lower Devonian. Uppermost Downton and Lowest Ditton Groups, Anglo-Welsh region (see Text-fig. 1).

Referred material. SRCH.G: 213 from Devil's Hole, 13 from Little Oxenbold, 6 from Earnstry Brook, 2 from Barnsland Farm Quarry, 1 from Oak Dingle; NMW: 2 from Cusop Dingle, 1 from Lydney and 3 from Manorbier Bay; material in the BMNH, BGS(GSM), and BU. This material consists of 27 dorsal discs, 14

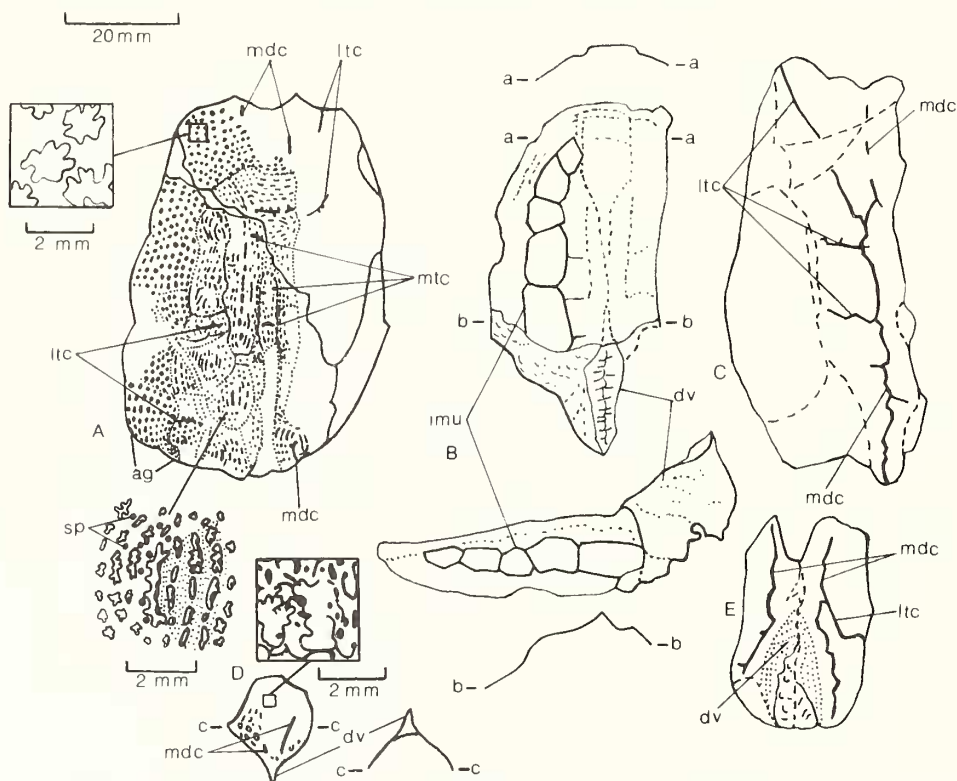
TABLE 1. Maximum dimensions of adult *Phialaspis symondsi* plates in millimetres. Abbreviation: pop, post-oral process.

	Range			Average		
	Length	Width	Ratio of width to length	Length	Width	Ratio of width to length
Dorsal discs	50-70	40-60	0.67-0.96	60	49	0.80
Orbital plates	26-34	12-22	0.44-0.56	30	16	0.52
Pineal plates	9-20	10-20	0.85-1.33	14	15	1.07
Rostrums	13-17	21-24	1.23-1.84	15	22	1.46
Branchio-cornuals	60-80	35-37	0.43-0.55	68	35	0.51
Ventral discs	68-100	42-64	0.54-0.75	81	50	0.61
Lateral plates + pop	26-43	14-24	0.48-0.61	36	20	0.56
Lateral plates - pop	20-31	16-23	0.67-0.90	25	19	0.76
Curvital dimensions						
Dorsal discs	51-77	50-74	0.76-1.08	64	60	0.93
Branchio-cornuals	94-116			100		
Ventral discs	69-101	44-74	0.61-0.78	83	59	0.71

dorsal vanes, 20 orbital plates, 10 pineal plates, 7 rostral plates, 26 branchio-cornual plates, 74 ventral discs, 20 lateral plates, 5 oral plates, plus scales and fragments.

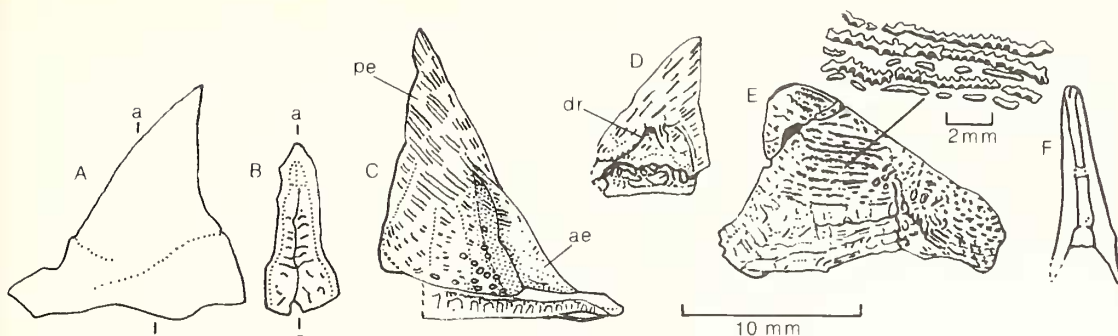
Diagnosis. As for genus.

Description. The dorsal disc (Pl. 1, figs 1 and 2; Pl. 2, fig. 2; Text-fig. 2) is highest and widest about halfway along its length. Its lateral margins are gently scalloped, and the anterior margin is sometimes angled and slightly indented to match the contact with the posterior margin of the pineal plate and the dorso-posterior margins of the orbital plates. The two lateral rows of units are most pronounced at the posterior of the first, most medially-placed row, and along the second row, internal impressions marking their edges can often be seen (Pl. 1, fig. 2; Text-fig. 2B). The cancellae are enlarged under the apex of each unit causing the exoskeleton



TEXT-FIG. 2. *Phialaspis symondsi* (Lankester), dorsal discs. A, part superimposed on counterpart to show ornamentation and incomplete sensory canals, SHRCM.G08137/1-2. B, incomplete and mainly internal mould in plan and lateral views. a-a, b-b, lines of cross section, SHRCM.G08138. C, part superimposed on counterpart to show sensory canal system, SHRCM.G08139/1-2. D, incomplete juvenile showing developing ornament. c-c, line of cross section, SHRCM.G08140. E, incomplete specimen with part superimposed on to counterpart to show sensory canal system, SHRCM.G08141/1-2. Abbreviations: ag, adult growth region; dv, dorsal vane; imu, internal impressions of units; ltc, lateral transverse commissure; mdc, medial dorsal longitudinal canal; mtc, medial transverse commissure; sp, sensory pore.

to swell from 1 to 2 mm in thickness. With the exception of the large tubercle or frequently large tubercles, capping the apex, the tubercles are small and irregular on the units. This contrasts with the larger and more equilateral tubercles found on the peripheral adult zone (Text-fig. 2A), where a longitudinal fold can sometimes be observed on each lateral side of the larger dorsal discs. This is so vestigial that it could hardly be described as a row of units.



TEXT-FIG. 3. *Phialaspis symondsii* (Lankester), dorsal vanes. A, lateral view SHRCM.G08142. B, cross section at a-a. C, short high specimen, SHRCM.G08143. D, adolescent specimen, SHRCM.G08144. E, long low specimen, showing ornamental details, SHRCM.G08145. F, ditto, posterior view. Abbreviations: ae, anterior element; dr, developing region; pe, posterior element.

The dorsal vane (Pl. 1, figs 3-5; Text-fig. 3) is triangulate and varies in proportion, ranging from 34 mm long \times 21 mm high to 19 mm long \times 26 mm high and is 7-10 mm thick at its base. Its two specialized units are often in tandem, with a doubled and thickened cancellous layer which narrows towards the tip and divides at the base to merge with the disc. The rear unit is normally largest. However, the dorsal vane of SHRCM.G08137 (Pl. 1, fig. 6) has an atrophied rear unit, and is mainly formed from the front unit.

Although broken at its anterior end, the dorsal vane SHRCM.G08140 (Pl. 1, fig. 3; Text-fig. 3D) is small, only 17 mm, in height. A depressed region running longitudinally just above its base may indicate an area of growth.

An incomplete and immature dorsal disc SHRCM.G08140 measures 17 mm long \times 24 mm double half width (Pl. 2, fig. 2; Text-fig. 2D). Its dorsal vane is shown in section and is 5 mm high \times 3 mm thick at the base. The medial longitudinal sensory canals have been exposed and are much closer together than on the larger dorsal discs. All levels of its exoskeleton were present. The surface is pitted with openings on the more complete left lateral and anterior edges. This grades inwards with developing tubercles (Text-fig. 2D) to well-formed large tubercles not arranged in cyclomoriform patterns.

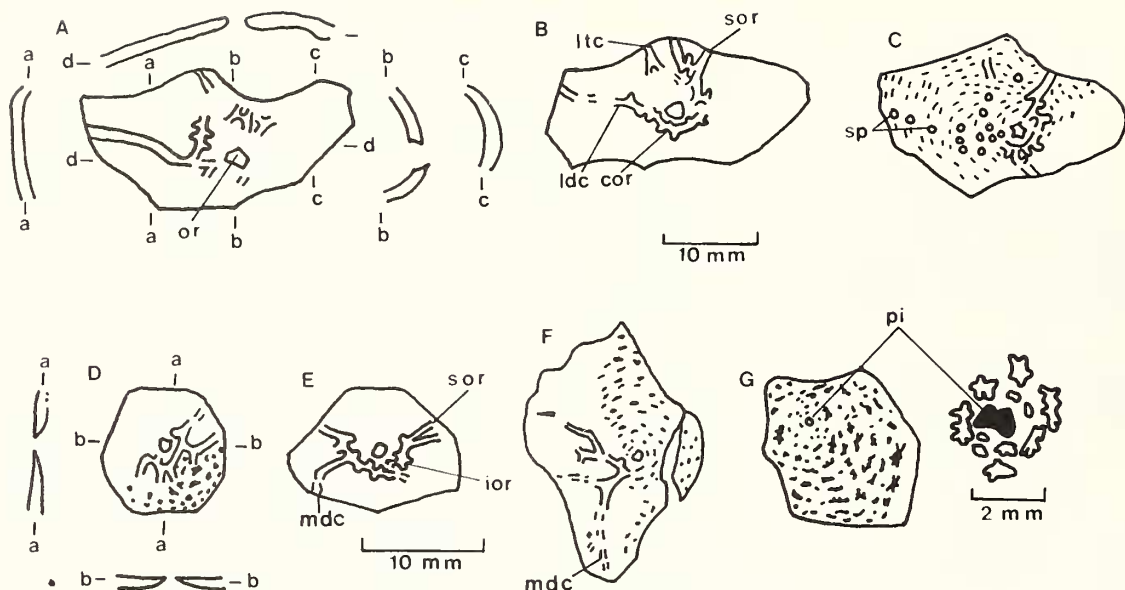
The orbital plates (Pl. 2, fig. 1; Text-fig. 4A-C) are elongate and irregularly diamond-shaped, with usually concave dorsal edges to accommodate the pineal plate. They are curved to present dorsal and lateral sides towards the front, and become flattened towards the back to slope at a dorso-lateral angle. The orbital opening ranges from 2 to 3 mm in diameter; it is on the angle of the dorso-lateral fold, and is usually slightly nearer the anterior edge of the plate than the posterior.

The pineal plate (Pl. 2, fig. 3; Text-fig. 4D-G) is distinguished by its flat and more or less rhomboid shape. There is a centrally placed pineal foramen, which is approximately 1 mm in diameter. The tubercles on the pineal and orbital plates are arranged in concentric rings around the pineal and orbital openings.

The dorsal side of the rostrum (Pl. 2, fig. 6; Text-fig. 5C) is rounded and highest at the posterior edge which is three-pointed, with two concave edges which would have accommodated the front of the orbital plate. The plate tapers towards a tip formed by large horizontally running tubercles.

The ventral pre-oral surface (Pl. 2, fig. 4; Text-fig. 5A) has a raised, flat central region, which probably represents an area of a similar kind to the pre-oral field found on certain pteraspidiiforms. With the exception of several long tubercles traversing the anterior half, it is ornamented with small and atrophied tubercles. Posterior to the pre-oral surface and rimmed with a maxillary flange on the angle of ascent, the pre-oral wall ascends vertically to join the posterior undersurface of the plate. The basal laminated layer on the posterior undersurface of SHRCM.G08161 (Text-fig. 5A) is folded and contorted on each side of a shallow median groove.

The larger specimens have proportionally longer pre-oral regions. On the smallest rostrum, NMW88.32G. (Pl. 2, fig. 5; Text-fig. 5D), the pre-oral region is 0.28 times the length and 0.60 times the width of the pre-oral region of SHRCM.G08161. It is broken along its posterior edge, and has all exoskeletal layers present. Its small size and proportions indicate it was from an immature animal. A strong depression on each side of the pre-oral surface shows regions of possible active growth. The basal laminated layer of the posterior undersurface, along its junction with the pre-oral wall, is perforated with vascular foramina often set within large depressions (Text-fig. 5D) which appear to match the contorted conditions found in this region on SHRCM.G08161.



TEXT-FIG. 4. *Phialaspis symondsii* (Lankester). A-C, orbital plates; A, right plate, part superimposed on counterpart to show sensory canal system, a-a, b-b, c-c, d-d, lines of cross section, SHRCM.G08147/1-2; B, right plate showing sensory canal system, NMW88.32G.2; C, right plate, part superimposed on counterpart to show ornamentation and sensory canal system, SHRCM.G08146/1-2. D-G, pineal plates: D, small plate, part superimposed on counterpart to show part of sensory canal system, a-a, b-b, lines of cross section, SHRCM.G08148/1-2; E, small plate, part superimposed on counterpart to show sensory canal system, SHRCM.G08149/1-2; F, fragmentary large plate, part superimposed on counterpart to show part of sensory canal system, SHRCM.G0815/1-2; G, fragmentary large plate showing pineal opening and ornamental details, SHRCM.G08151. Abbreviations: cor, circum-orbital canal; ior, inter-orbital canal; ldc, dorsal longitudinal canal; lrc, lateral transverse commissure; mdc, medial dorsal longitudinal canal; or, orbit; pi, pineal organ; sor, supra-orbital canal; sp, sensory pores.

The branchial opening, located about three-fifths of the way along the length of the branchio-cornual plate (Pl. 3, figs 4 and 5; Text-fig. 6) is dorsally facing and ovate, and ranges in size from 8×4 mm to 11×7 mm.

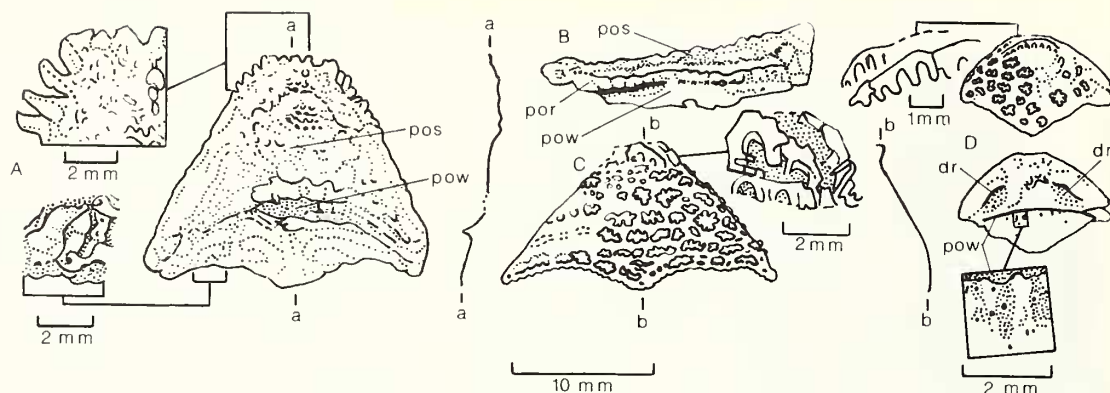
The lateral keel embraces the lateral side of the branchial duct and encloses the front of the branchial opening. Its vascular cancellous layer is greatly thickened and individually variable, ranging from 5-12 mm wide \times 4-10 mm thick regardless of the size of the rest of the plate. Elongated and longitudinally running rows of tubercles are found on both sides of this region. On its lateral edge, closely spaced, 1 mm thick tubercles overlie smaller primary tubercles (Text-fig. 6B). Occasionally, there are regions of abrasion on the ventral side (Text-fig. 6D).

The lateral vane occupies from the back, one half to one third the length of the branchio-cornual plate and joins the lateral keel. It is solid, triangulate, and dorso-ventrally flattened, with two greatly thickened vascular cancellous layers. Measuring 7 mm thick at its base on SHRCM.G08194, it forms the postero-lateral edge of the branchial opening. The whole vane is tilted postero-laterally, with an elongated region of small and

EXPLANATION OF PLATE I

Figs 1-6. *Phialaspis symondsii* (Lankester), lower Devonian, Welsh Borderland. 1, 2, 6, dorsal discs, $\times 2$; 1, SHRCM.G08166/1, dorsal view of external mould; 2, SHRCM.G08243/1, dorsal view of small internal mould showing impressions; 6, SHRCM.G08166, lateral view of silicon rubber impression showing malformed dorsal vane. 3-5, dorsal vanes, $\times 2$; 3, SHRCM.G08140, external cast of immature vane; 4, SHRCM.G08143, external cast; 5, SHRCM.G08145, external cast.





TEXT-FIG. 5. *Phialaspis symondsii* (Lankester), rostral plates. A, ventral view showing details of tip and posterior undersurface, a-a, line of cross section, SHRCM.G08160. B, fragmentary specimen, showing pre-oral wall and part of pre-oral surface, SHRCM.G08161. C, dorsal view showing ornamentation, b-b, line of cross section, SHRCM.G08162. D, immature specimen, part superimposed on to counterpart to show dorsal side with details of ornamentation, and ventral side with details of posterior under surface, NMW88.32G.1a/b. Abbreviations: dr, developing region; por, pre-oral rim/maxillary brim; pos, pre-oral surface; pow, pre-oral wall.

irregularly shaped tubercles running from the tip to the branchial opening and dividing the dorsal side. On the antero-dorsal side and edge, the tubercles have a tendency to form weak ornamental units and run in rows around the postero-dorsal and ventral sides. Towards the tip, they become elongated and reach up to 1 mm in thickness. The lateral vane is usually terminated at the back by a cyclomorform unit, which forms a horizontal flange (see Text-fig. 6A) measuring 10 mm long \times 5 mm wide on SHRCM.G08153 and SHRCM.G08154. Where the branchial-cornual plate slopes upwards to meet the lateral edge of the dorsal disc, it is composed of a longitudinal row of units (Text-fig. 7B,E). These cover the dorsal side of the branchial duct, encircle the medially facing side of the branchial opening, and are terminated posteriorly by a large unit (Text-fig. 6A,D). They often leave internal impressions marking their edges (Pl. 3, fig. 4; Text-fig. 6B). On the basal laminated layer of SHRCM.G08155 growth ridges run longitudinally between the units and the lateral keel (Text-fig. 6E).

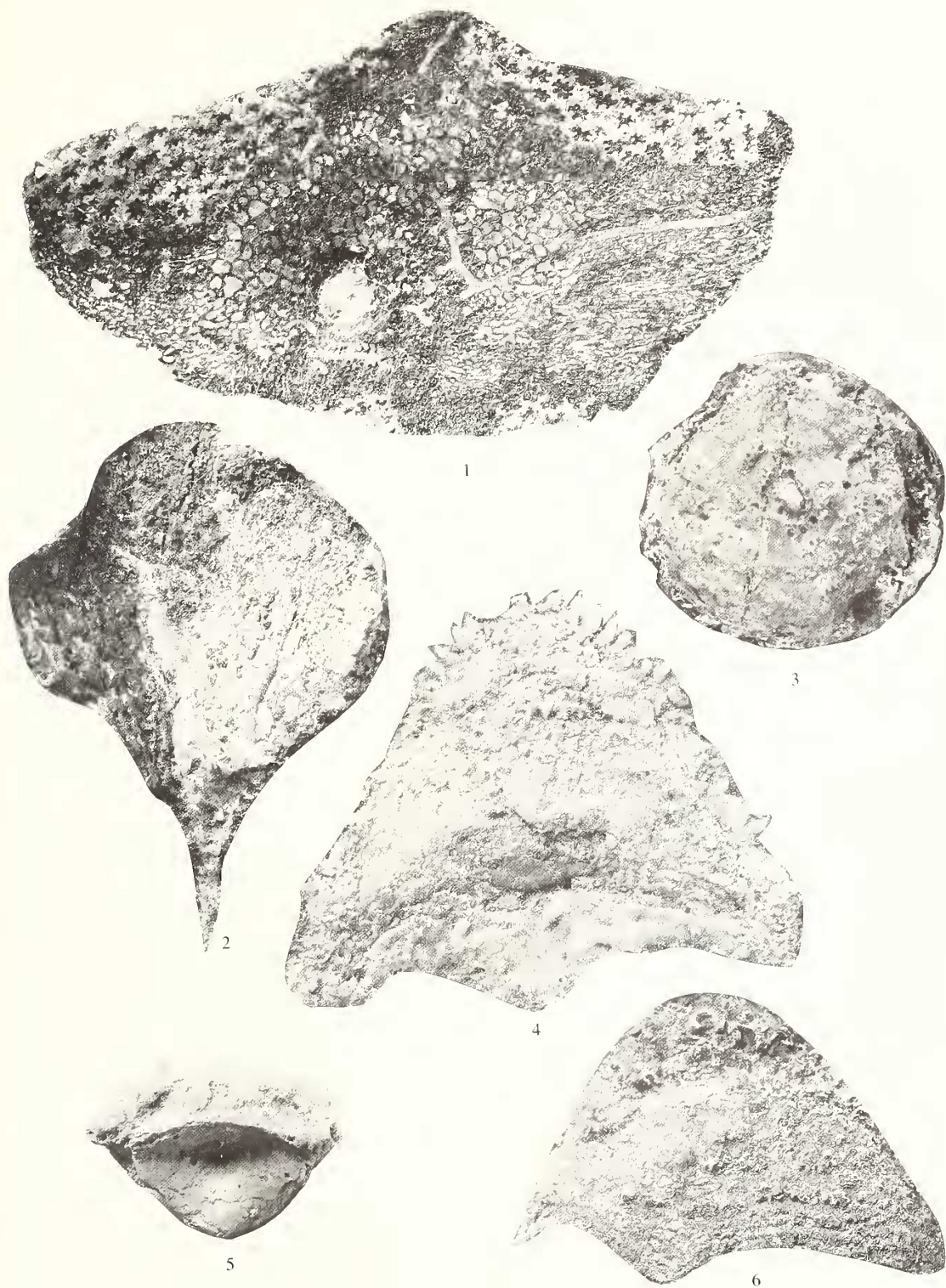
The ornament on the ventral side of the branchio-cornual plate (Text-fig. 6C) curves transversely from the front of the lateral vane, to run parallel with the ventral edge, which is concave to accommodate the lateral edge of the ventral disc. A zone of growth runs parallel with the ventral and dorsal anterior edges, which are angled to match the ventro-posterior edge of the orbital plate and the posterior edge of the lateral plate.

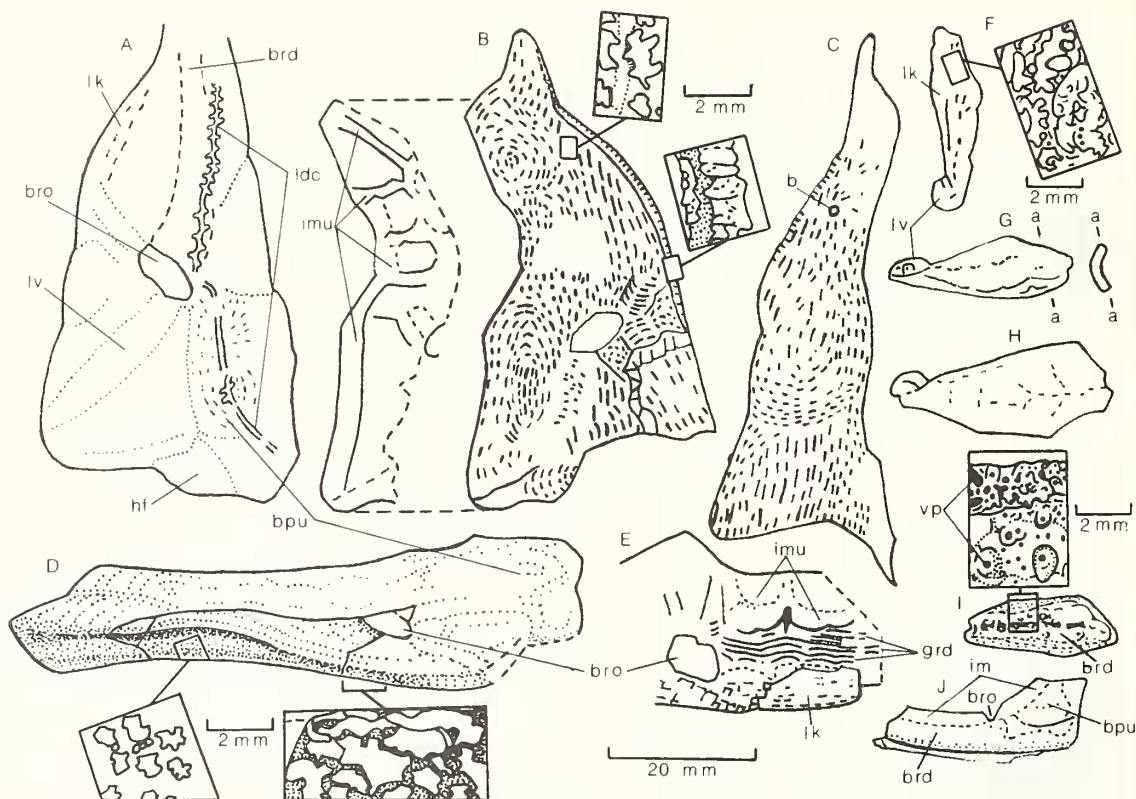
Three elongate and approximately diamond-shaped plates (Pl. 3, figs 1 and 2; Text-fig. 6F,H,I) appear to represent juvenile branchio-cornual plates. Their sizes are: SHRCM.G08157 33 mm long \times 13 mm wide; SHRCM.G08156 26 mm long \times 10 mm wide; SHRCM.G08158 21 mm long \times 8 mm wide. Each is bowed along its length, angled at its front, and tapered towards the back, where a region about 5 mm long projects about 2.5 mm from the lateral side of the plate. This apparently represents the developing lateral vane.

SHRCM.G08156 has been prepared to show typical *P. symondsii* tubercles in various stages of eruption and development (Text-fig. 6F). The inner surface of SHRCM.G08158, shows recently enclosed spaces which form blister-like regions with centrally-placed pores. A 1–2 mm wide margin around the edges is a maze of openings surrounded by enclosing basal laminated growth (Pl. 3, fig. 3; Text-fig. 6I). The longitudinal row of units is

EXPLANATION OF PLATE 2

Figs 1–6. *Phialaspis symondsii* (Lankester), lower Devonian, Welsh Borderland. 1, SHRCM.G08147/2, right orbital plate, mostly internal view. 2, SHRCM.G08140, immature dorsal disc, in part external mould. 3, SHRCM.G08250, cast of pineal plate. 4, SHRCM.G08160, cast of ventral surface of rostrum. 5, NMW88.32G.1a, cast of ventral surface of immature rostrum. 6, SHRCM.G08162/1, cast of dorsal surface of rostrum. All \times 4.





TEXT-FIG. 6. *Phialaspis symondsii* (Lankester), branchio-cornual plates. A, left plate, dorsal side with part superimposed on counterpart, showing sensory canal system, SHRCM.G08152/1-2. B, right plate, dorsal side showing ornamentation, with dorsal half of counterpart showing inner surface, SHRCM.G08153/1-2. C, right plate, ventral side with part superimposed on counterpart, SHRCM.G08154/1-2. D, left plate, lateral view showing details of worn ornament, BMNH31146. E, fragmentary right plate, lateral view of inner surface, SHRCM.G08155. F, G, juvenile right plate; F, ventral view with detail of ornamentation; G, lateral view; a-a, line of cross section, SHRCM.G08156. H, juvenile right plate, lateral view, SHRCM.G08157. I, juvenile left plate, showing inner surface, SHRCM.G08158/1-2. J, 'adolescent' left plate, lateral view, mainly internal, SHRCM.G08159. Abbreviations: b', bite; bpu, large posterior unit; brd, branchial duct; bro, branchial opening; grd, growth ridges; hf, horizontal flange; im, inset margin; imu, internal impressions of units; ldc, lateral dorsal longitudinal canals; lk, lateral keel; lv, lateral vane; vp, vascular pores.

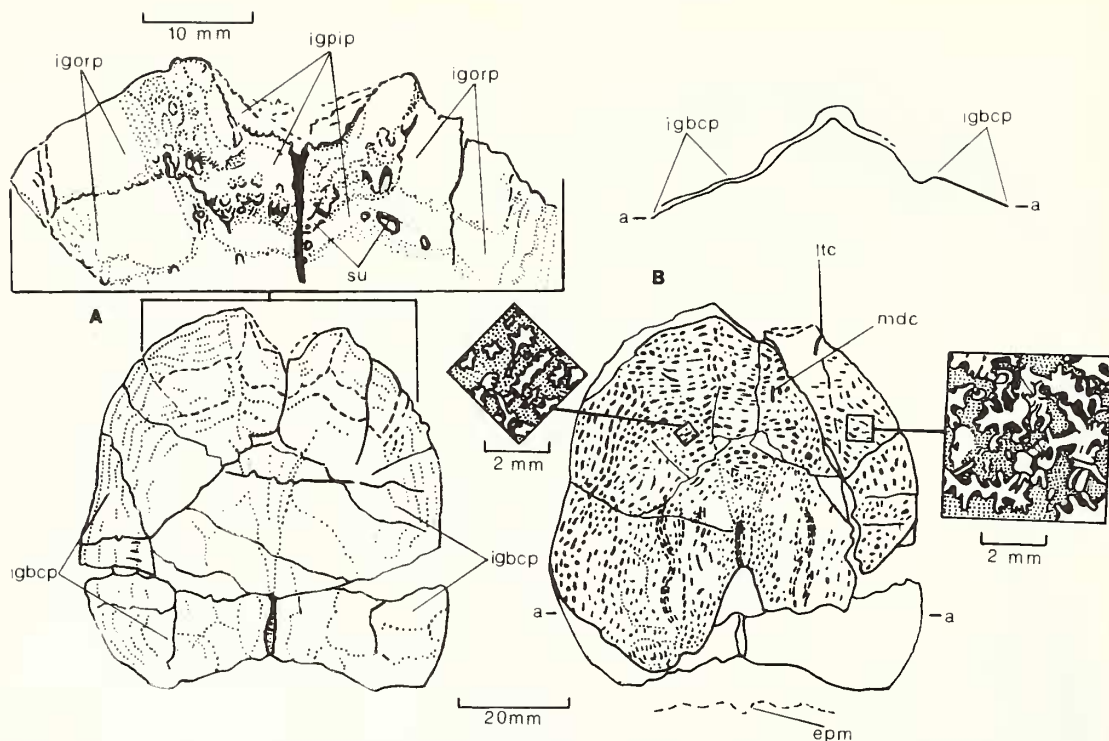
missing from these plates, and they are much flatter than the adult branchio-cornual plates. Nevertheless, their branchial ducts run their entire length, which shows that the branchial openings were posteriorly placed and not enclosed. Although the superficial layer was destroyed during preparation, the lateral side of SHRCM.G08157 is 4 mm in thickness, corresponding to the enlargement of the lateral keel.

SHRCM.G08159 (Text-fig. 6j) is an internal mould of an early stage of development of a branchio-cornual

EXPLANATION OF PLATE 3

Figs 1-5. *Phialaspis symondsii* (Lankester), lower Devonian, Welsh Borderland, branchio-cornual plates. 1, SHRCM.G08158/1, cast of inner surface of immature left plate, $\times 4$. 2, SHRCM.G08156, cast of ventral surface of immature right plate, $\times 4$. 3, detail of 1, $\times 10$. 4, SHRCM.G08153/1, dorsal view of right plate, in part internal mould, $\times 2$. 5, SHRCM.G08152/2, dorsal view of external mould of left plate, $\times 2$.



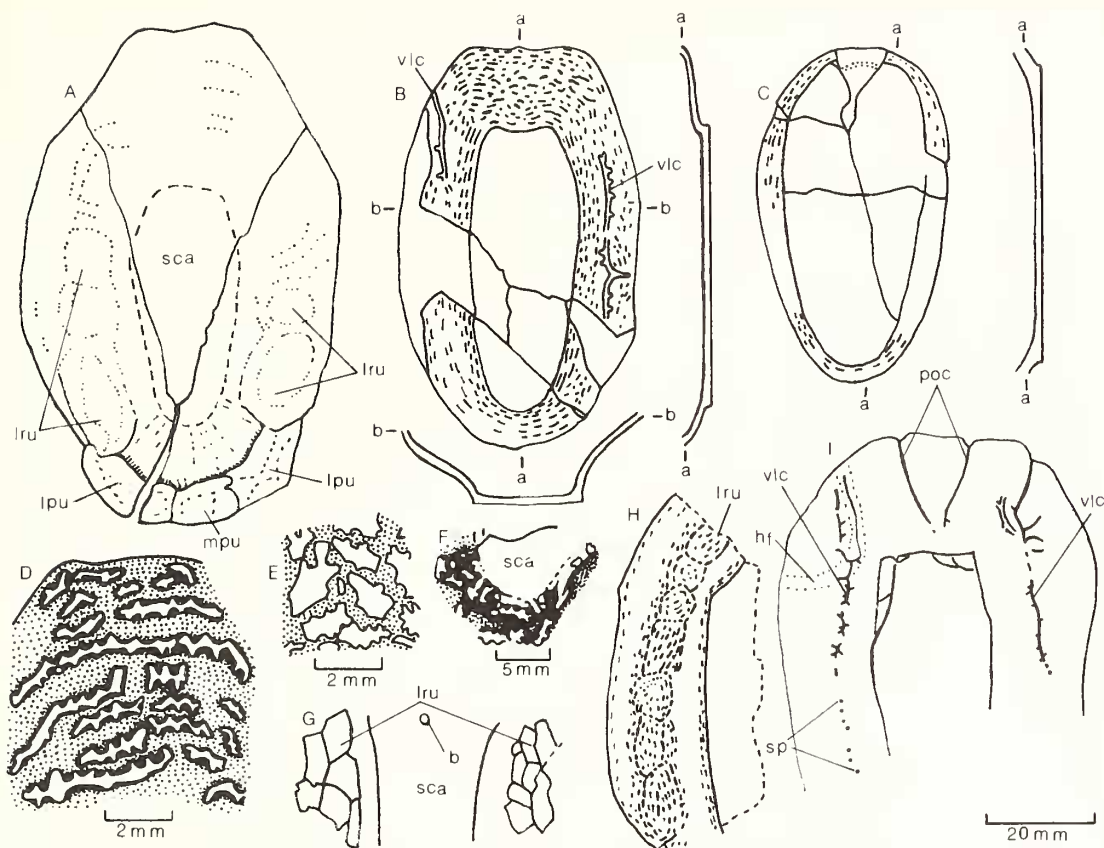


TEXT-FIG. 7. *Phialaspis symondsii* (Lankester), dorsal shield, SHRCM.G08164/1-2. A, internal plan view, with detail of anterior. B, part superimposed on to counterpart to show ornamentation, a-a, line of cross section. Abbreviations: epm, estimated position of posterior margin; igbcp, regions of intergrowth between dorsal disc and branchio-cornual plate; igorp, regions of intergrowth between dorsal disc and orbital plate; igpip, regions of intergrowth between dorsal disc and pineal plate; ltc, lateral transverse commissure; mdc, medial dorsal longitudinal canal; su, sutures.

plate. Although the whole plate only measures 30 mm long, its branchial duct is strongly dorso-ventrally folded as in adult specimens. A cross-section at the front shows all levels of the exoskeleton to be present. The large dorsal posterior unit is present, and is estimated to be two-thirds the size of the equivalent area on the adult plates. A depressed margin, 1-2 mm wide, around its dorsal and posterior edges, and running along the dorsal side of the branchial duct, appears to show regions of active outward growth. An open-ended notch 2 mm wide dissects the margin at the anterior of the posterior unit and appears to represent the start of the enclosure of the branchial opening.

An incomplete dorsal headshield, SHRCM.G08164 (Pl. 4, figs 1 and 2; Text-fig. 7), which is somewhat distorted by compression, consists of the dorsal disc, the inner halves of the branchio-cornual plates, the back of the pineal plate and the dorso-posterior part of the orbital plates, with the omission of the pineal, orbital, and branchial openings. In contrast to the tubercles found in the regions of adult growth of isolated dorsal discs, the tubercles in the regions of adult growth of SHRCM.G08164 vary considerably in size and shape (Text-fig. 7B). Prior to the formation of peripheral adult growth, the dorsal disc acquired the longitudinal units of the branchio-cornual plates, then fused with the back of the pineal plate and the dorso-posterior part of the orbital plates, where sutures can be observed on the inner surface (Text-fig. 7A). As there is no evidence of adult growth on the dorsal edges of the branchio-cornual plates of *P. symondsii*, it appears that during adulthood, the dorsal disc SHRCM.G08164 encroached and intergrew with the longitudinal units of the branchio-cornual plates. Due to a large range in size, it would appear that the pineal and orbital plates of *P. symondsii* were capable of adult growth, and probably on SHRCM.G08164, they contributed to the intergrowth and kept the encroachment of the dorsal disc in check.

In the ventral discs (Text-fig. 8), the flat central area stands proud by 1-2 mm and its surface consists of a



TEXT-FIG. 8. *Phialaspis symondsii* (Lankester), ventral disc. A, internal view, showing attached posterior units, SHRCM.G08165. B, external view showing sensory canal system, a-a, b-b, lines of cross section, SHRCM.G08166/1-2. C, immature plate, a-a, line of cross section, SHRCM.G08167/1-2. D, detail of ornament on left anterior corner, SHRCM.G08168. E, detail of worn ornament on the anterior, BMNH46712. F, abraded posterior, SHRCM.G08169; G, transverse view across midline, showing part of abnormal longitudinal rows of units, SHRCM.G08170. H, part of left side showing longitudinal rows of units, SHRCM.G08171/1, specimen developed to show sensory canal system, SHRCM.G08171. Abbreviations: b', bite; hf, healed fracture; lpu, lateral posterior unit; lru, longitudinal row of units; mpu, medial posterior unit; poc, post-oral sensory canal; sca, smooth central area; sp, sensory pores; vlc, ventral longitudinal sensory canal.

smooth sheet of dentine. Regardless of the size of the rest of the disc, it varies considerably in size and proportions, ranging in length from 31 to 60 mm, and in width from 11 mm to an estimated and exceptional 40 mm in BU759. The posterior edge in SHRCM.G08169 is worn, and the adjacent tubercles are abraded and merge with the smooth dentine (Text-fig. 8F).

The tubercles of the ventral disc, in contrast to those of the dorsal disc, are usually of a similar size and normally moderately elongated. Tarlo (1962) recognised that bands of ornamented growth joined each lateral side of the smooth central region to a row of longitudinally running units. These units are cyclomoriform and raised centrally. Although internal impressions marking their edges are sometimes observed, they often protrude internally. There are usually five or more a side, and in SHRCM.G08170 there are two rows crowded together on each side (Text-fig. 8G). A single unit can range in size from 4-15 mm long \times 4-10 mm wide.

In certain specimens of ventral discs, the ornament at the front runs horizontally, matching underlying growth ridges. In other cases, it runs at right angles to the growth ridges, before curving round the anterior edges of the longitudinal rows of units, where on SHRCM.G08168 the tubercles join together to become

elongated (Text-fig. 8D). This region on BMNH46712 has broadened and abraded tubercles (Text-fig. 8E). The flow of ornament running from the posterior of the smooth central region is also variable, but does not overlie any growth ridges.

Three units forming the posterior end of the ventral disc and uniting the two longitudinal rows of units are only observed clearly as internal impressions on SHRCM.G08165 (Pl. 4, fig. 4; Text-fig. 8A), and probably contacted the antero-ventral ridge scale and the two antero-ventral scales. The medial posterior unit measures 7 mm long \times 9 mm wide and the two lateral posterior units both measure 11 mm long \times 17 mm wide. As they flatten out at an angle from the vaulted posterior end of the disc, it is likely that they would have been lost after death, and were seemingly often independent of the disc in the younger animals.

Four specimens of immature ventral discs are represented by smooth areas with narrow ornamented margins and no attached units. Each central area is of adult proportions, but as observed on SHRCM.G08167 (Pl. 4, fig. 3; Text-fig. 8C), it rests only slightly proud of the rest of the disc. The anterior and posterior ends of the discs are observed to be flattened internally by a thickening of the cancellous layer.

A specimen (BU77) described by Wills (1935) as cf. *Ctenaspis*, is actually a fragmentary ventral disc from *P. symondsii*. With the exception of a small region of smooth dentine measuring 1 \times 2 mm, the superficial layer is missing, leaving the cancellae exposed.

As White (1946) found on *T. pococki*, *P. symondsii* had two lateral plates. The lateral plate is approximately triangular in shape (Pl. 5, figs 2 and 5; Text-fig. 9A–D). It is widest at its anterior end, and tapers towards its posterior edge where it met the branchio-cornual plate. The plate is folded, forming anterior, lateral, and ventral sides, and it is deepest at their junction. The bulk of the plate is ventral in position, where it is flattest. One edge is concave to embrace half of the anterior edge of the ventral disc. On the opposite edge, the plate is folded longitudinally at an angle of 60–90°, to form the 3–4 mm wide laterally facing side, which is angled to meet the ventral edge of the orbital plate. The anteriorly facing side folds inwards at between 20° and 50° from the main body of the plate. It is cradled by a concave region, which at one end forms a projection that would have met the postero-ventral part of the rostrum, and at the other end forms either a truncated mesial edge, or a post-oral process (Text-fig. 9A,C). The post-oral process is partly square in outline, flattened at its free end, and measures about 5 mm long \times 10 mm wide. It is too short to occupy the space between the lateral plates, the front of the ventral disc, and the oral region, and must therefore have been paired.

About one third of the lateral plates collected from Devil's Hole have post-oral processes, but the rest show no sign of this structure and must have possessed separate post-oral plates. Older animals may have fused plates. Although the lateral plate, SHRCM.G08174 (Pl. 5, fig. 5; Text-fig. 9D), has an exoskeleton of adult thickness, it measures 19 mm long \times 10 mm wide, and is so small that it must represent an immature plate, yet it possesses a well-formed post-oral process.

The ornament on the lateral plates is cyclomoriform, and the post-oral process was formed from a separate cyclomoriform unit. The tubercles in some specimens (Text-fig. 9A) are enlarged and joined together, and tubercles occasionally run at right angles to the main ornamental direction.

Because of their large size, it seems that two anterior lateral plates and one median oral plate were the full complement of oral plates present in *P. symondsii*.

The posterior end of the median oral plate seems to have been as wide, if not slightly wider than the posterior margin of the oral cavity, and somewhat longer than the length of the oral cavity. Therefore it would appear to have rested inside the mouth, where, laterally and posteriorly, it was overlapped by the anterior lateral plates. It ranges in width from 16 to 11 mm, in length from 14 to 12 mm, and is about 6 mm high. It is scoop-shaped, and is ornamented on its outer side and smooth on its inner side and edges (Pl. 5, fig. 4; Text-fig. 9E,F). The inner side (Text-fig. 9F) has an elongated and gently convex central area, which strengthens and widens towards the back. The inner side behind the edge turns outwards to form a narrow lip, which is matched by a thickening of the exoskeleton. On the outside the tubercles are small and narrow and they generally run longitudinally, although they sometimes curve and run at right angles to the main direction. The ornament is abraded in places, in particular on the right lateral side of SHRCM.G08177, and there is a large callus 5 mm

EXPLANATION OF PLATE 4

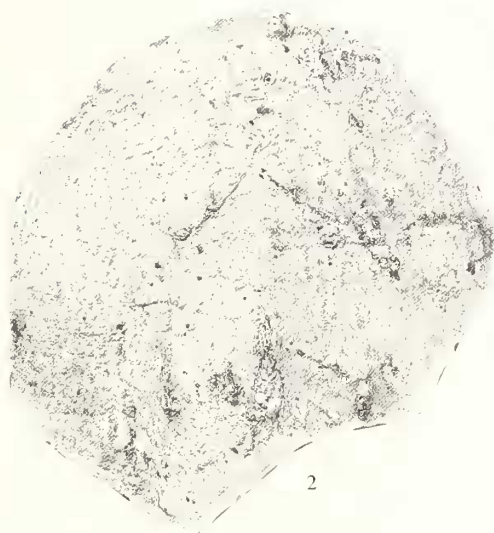
Figs 1–4. *Phialaspis symondsii* (Lankester), lower Devonian, Welsh Borderland. 1 and 2, SHRCM.G08164/1/2, dorsal headshield, dorsal views of internal mould and silicon rubber impression of external surface, respectively. 3 and 4, ventral discs; 3, SHRCM.G08167/1, external mould of immature disc; 4, SHRCM.G08165, internal view of cast. All \times 1.



1



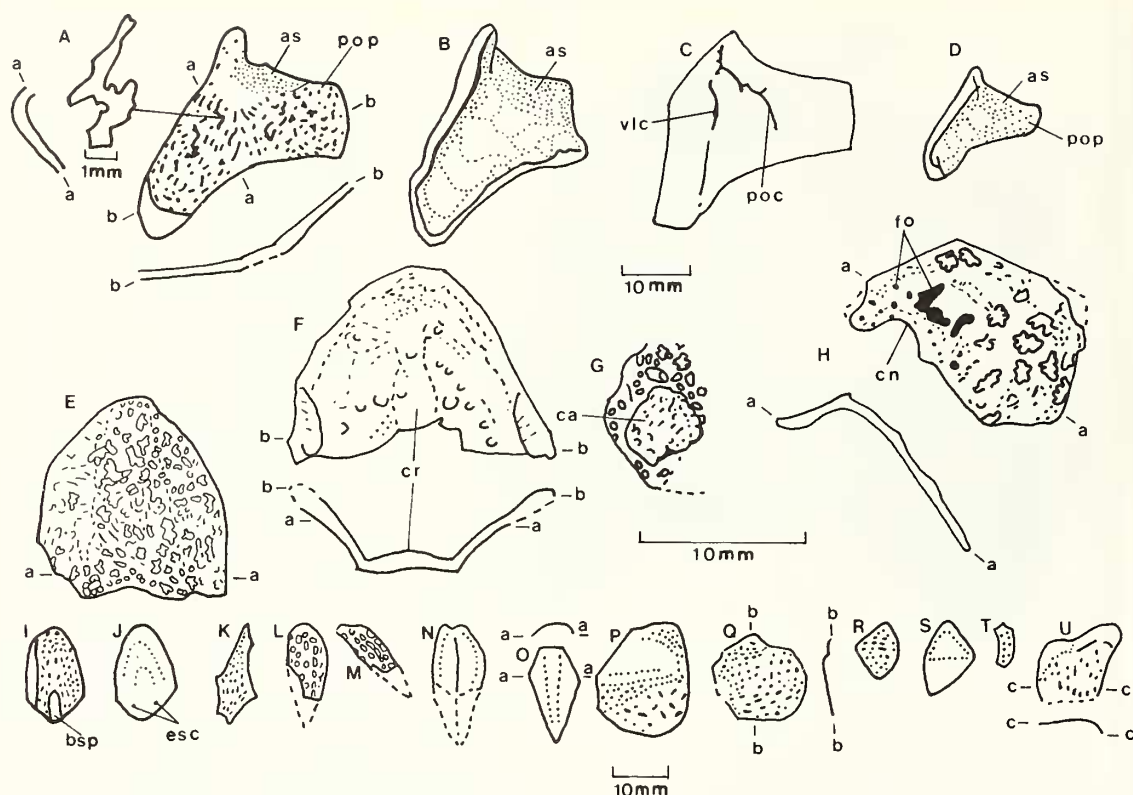
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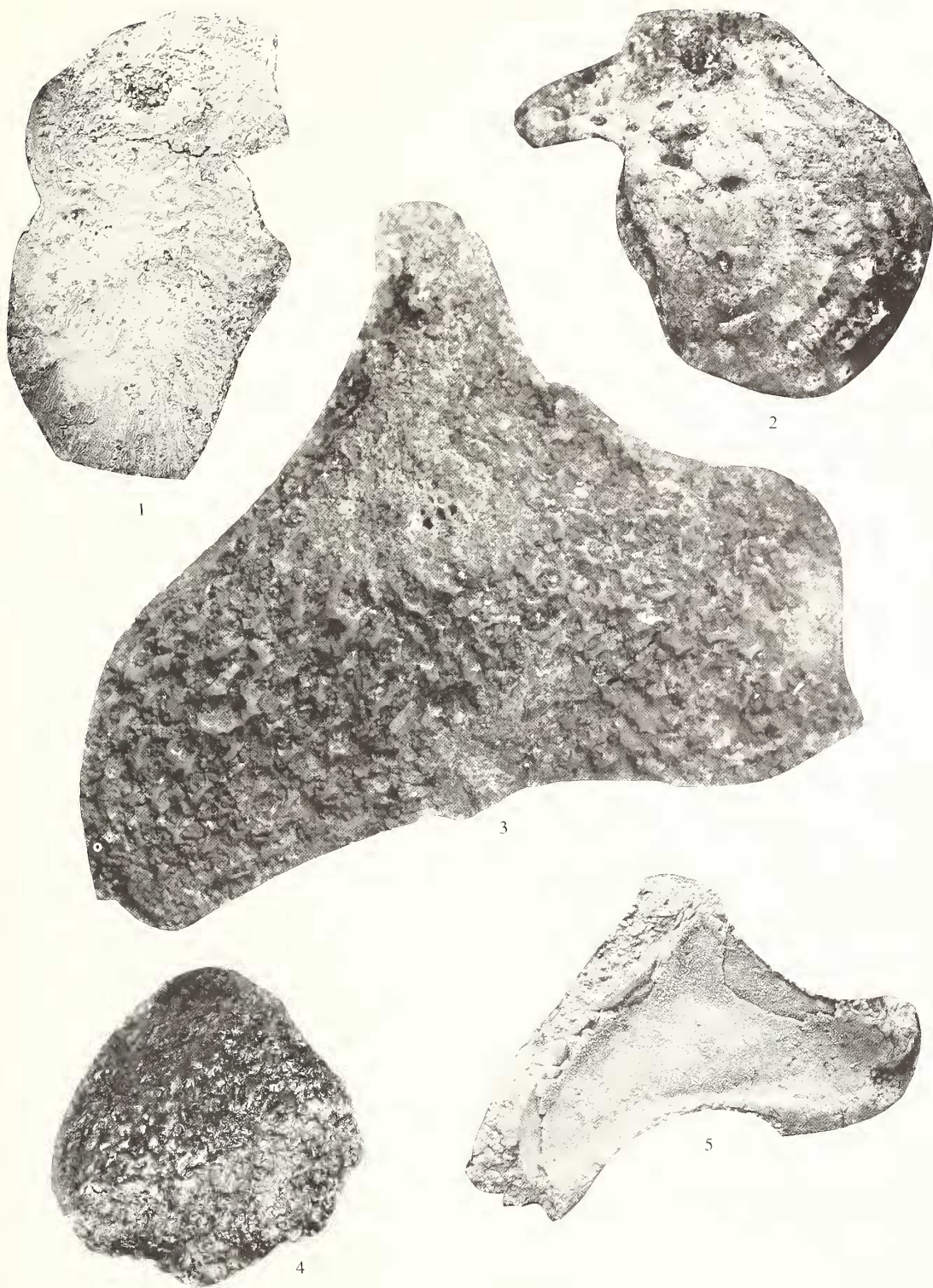


TEXT-FIG. 9. *Phialaspis symondsii* (Lankester), A-D, lateral plates; A, external view of right plate, showing orna-mentation, a-a, b-b, lines of cross section, SHRCM.G08173/1-2; B, internal view of left plate, without post-oral process, SHRCM.G08176/1-2; C, right plate developed to show sensory canal system, SHRCM.G08175; D, internal view of immature left plate, SHRCM.G08174. E-H, oral plates; E, internal view of median oral plate; F, ditto, external view, a-a, b-b, lines of cross section, SHRCM.G08177/1-2; G, right posterolateral corner of median oral plate, showing region of abrasion, SHRCM.G08178. H, external view of left anterior lateral plate, c-c, line of cross section, SHRCM.G08179. I-U, scales; I-K, dorsal ridge scale, SHRCM.G08180/1-2; I, external view; J, internal view; K, lateral view; L-M, ventral ridge scale, SHRCM.G08181; L, external view; M, lateral view; N-O, internal views of ventral ridge scales, a-a, line of cross section, SHRCM.G08182, 08183; P-Q, large flank scales, b-b line of cross section, SHRCM.G08190, 08191; R, external view of flank scale, SHRCM.G08185; S, internal view of flank scale, SHRCM.G08184; T, ?caudal scale, SHRCM.G08187; U, incomplete ?ventral lateral scale, c-c, line of cross section, SHRCM.G08189. Abbreviations: as, anterior side; bsp, broken spine; ca, calus; cn, concaved notch; cr, convex central area; esc, exit pores for sensory canals; fo, foramina; poc, post-oral sensory canal; pop, post-oral process; vlc, ventral longitudinal sensory canal.

EXPLANATION OF PLATE 5

Fig. 1. *Toombsaspis pococki* (White), lower Devonian, Welsh Borderland, BU.2098/1, cast of dorsal headshield, $\times 4$.

Figs 2-5. *Phialaspis symondsii* (Lankester), lower Devonian, Welsh Borderland. 2, SHRCM.G08179, cast of right anterior lateral plate. 3, SHRCM.G08173/1, cast of right lateral plate. 4, SHRCM.G08177/1, cast of median oral plate. 5, SHRCM.G08174, internal view of cast of immature left lateral plate. All $\times 4$.



long and 2 mm thick, at the posterior end of the right lateral side in SHRCM.G08178 (Text-fig. 9G). The worst of these abrasions appear to have been caused by friction against the anterior lateral plates.

The anterior lateral plate is represented by one specimen SHRCM.G08179 (Pl. 5, fig. 2; Text-fig. 9H). Although much larger, this resembles BMNH24788, a specimen that White (1946) described as possibly an anterior lateral plate from *T. pococki*. It measures 14 × 10 mm and is semicircular and bowed in shape. It rises to 4 mm, around a concave notch on one edge, and flattens towards the opposite edge. The inner surface is smooth, and the tubercles on the outer surface are progressively more abraded towards the raised region, where they are missing. The exoskeleton is pierced by foramina, which radiate in three rows around the concave notch. The largest of these foramina are ovate, 1 mm in diameter, and are angled to point towards the flattened part of the plate. These oral plates presumably lay freely edge to edge, with their raised concave notches lying antero-laterally and facing the anterior edges of the lateral plates. This supposition is based on the shape of the oral cavity, as manifested by its surrounding plates, and the shape and dimensions of the anterior lateral plates.

As White (1946) observed with *Phialaspis*, the sensory canal system was variable, irregular, often asymmetrical, and in *P. symondsi* sometimes segmented. It also ranged considerably in depth within the exoskeleton. Grooves underlying sensory canals can be seen with varying clarity on the internal moulds. These are not to be confused with impressions marking the edges of units (Text-figs 2B and 6B). In places, rows of pores can be traced across the external surface of several specimens (Text-figs 2A, 4C, 8I).

White (1946) considered that *T. pococki* had paired, medial and lateral dorsal longitudinal canals joined by medial and lateral transverse commissures, although he suggested that the lateral dorsal longitudinal canals may have been incomplete or sometimes absent. It is possible that the lateral transverse commissures were occasionally partly joined at their lateral extremities by a longitudinal canal, but I have found no evidence in *T. pococki* or *P. symondsi* to support the presence of lateral dorsal longitudinal canals in the positions suggested by White. Instead, it would appear that they were isolated, except at their anterior end, from the lateral transverse commissures, and are represented by the branchial canals described in *T. pococki* by White (1946). In *P. symondsi*, these run under the longitudinal rows of units on the branchio-cornual plates (Text-fig. 6A).

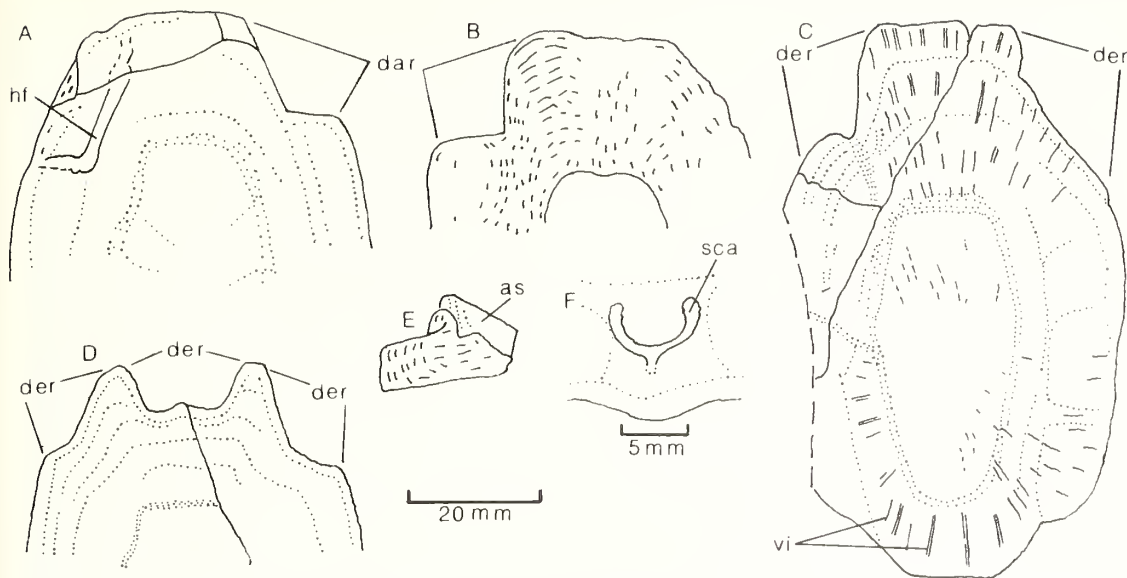
The inter-orbital canal forms a crescent on the pineal plate encircling the posterior and lateral sides of the pineal organ (Text-fig. 4E,F). It joins the medial dorsal longitudinal canals. On each side, it meets a supra-orbital canal and a transverse canal which run on to the orbital plate (Text-figs 4 and 13), and join before meeting the circum-orbital canal (Text-figs 4A–C, 13, 14). The circum-orbital canal completely encircles the orbit. Radiating from it, are the anterior lateral transverse commissure, the lateral dorsal longitudinal canal, and a canal which runs ventrally on to the lateral plate (Text-figs 4C and 9C) and joins the post-oral and ventral longitudinal canals. White (1946) observed no post-oral canals in the *P. symondsi* ventral discs he studied. This is often the case, as the post-oral canals were frequently short and confined to the lateral plates, although sometimes they were present on the ventral discs and V-shaped (Text-fig. 8I). As White noted, the ventral longitudinal canals underlaid the longitudinal rows of units and were varied, often segmented posteriorly (Text-fig. 8B,I).

Because specimens of the rostrum and anterior lateral plates are rare, no attempt has been made to expose possible sensory canals in these regions. However, no evidence has been found for sensory canals either leading to or on them, and it would appear that these were either absent or not linked to the main sensory canal system.

A variety of scales has been found, scattered thinly among the larger *P. symondsi* plates. Most are superficially pteraspid-like, but the anterior flank scales are proportionally much larger.

Dorsal ridge scales measure 8 mm long × 5 mm wide to 17 mm long × 16 mm wide. They are rounded and flattened anteriorly and rise towards the back to create an overlapping region where, although broken on SHRCM.G08177 (Text-fig. 9I–K), they appear to have been crowned with a low spine. The undersurface is gently dished, with two exit pores near the back for the medial dorsal longitudinal sensory canals. The ventral ridge scales range from 8 mm long × 4 mm wide to over 17 mm long × 9 mm wide. They are elongated and spinate (Text-fig. 9L–O), with a small anterior region of attachment angled at about 60° from a hollowed, posterior undersurface. This shows that they were considerably raised and possibly, overlapped strongly.

Several flank scales, including two very large specimens (Text-fig. 9P,Q), are asymmetrical and somewhat flattened, and range in size from 11 × 11 mm to 16 × 18 mm. A depressed region running across one anterior corner indicates an overlapped region, the majority of flank scales collected are smaller, ranging from 7 mm long × 8 mm wide to 10 mm long × 13 mm wide. They are diamond shaped (Text-fig. 9R,S) and folded longitudinally to leave a slightly raised posterior and a somewhat flattened anterior corner, suggesting regions of overlap. Several possibly incomplete, anterior ventral lateral scales are asymmetrical, elongated, and folded longitudinally, to present two unequal sides (Text-fig. 9U). They range from 15 mm long × 10 mm wide to over 15 mm long × 15 mm wide. Two small crescent scales are possibly caudal in origin (Text-fig. 9T).



TEXT-FIG. 10. *Phialaspis symondsii* (Lankester), regions of injury. A–D, on anterior parts of ventral discs; A,B,C, SHRCM.G3802/G08168/G08195.1–2 respectively; D, BGS GSM31380. E, deformed lateral plate, SHRCM.G08196. F, scar on longitudinal unit of ventral disc, SHRCM.G38197. Abbreviations: as, anterior side; dar, damaged region; der, deformed region; hf, healed fracture; sca, scar; vi, vascular impressions.

Injuries and predation scars. White (1946, figs 53 and 54) observed the impression of a healed fracture in the left anterior corner of the *P. symondsii* ventral disc BMNH194. The injury had healed perfectly showing, as White suggested, that the injury must have happened some time before the animal's death. Of ventral discs collected from Devil's Hole which were complete enough to observe the anterior portion, 44% showed injuries like the fracture described by White (Pl. 6, fig. 5), which suggests a common specific kind of injury. Although many of these injuries consist of healed fractures, on several specimens one or both antero-lateral corners are missing (see Pl. 6, figs 3–5; Text-fig. 10A–D). This shows a failure of the broken components to knit. In certain individuals (Text-fig. 10B), narrow regions of outward growth, running across these more severe injuries, show that the animals died soon after their occurrence. In contrast, other specimens (Text-fig. 10C,D) show a reasonable amount of post-injury plate growth. These injuries are extreme in the type specimen BGS(GSM)31380 (Text-fig. 10D), where both antero-lateral corners and a medially placed segment at the front are missing. A deformed, right lateral plate (Text-fig. 10E) has the usual concave contact edge with the ventral disc straight. This may correspond to the injuries on the ventral discs.

A ventral disc SHRCM.G08170 and a branchio-cornual plate SHRCM.G08154 (Text-figs 6G and 8C) are both pierced by a 1.5 mm wide circular hole. Tarlo (1966) observed a hole of a similar kind in the branchial plate of *Psammosteus praecursor*, which he considered was caused by a crossopterygian bite. It is possible that the holes in *P. symondsii* may have been caused by the bite of a large ischnacanthid. Much the same may apply to a well-healed, semi-circular scar on a longitudinal unit of the ventral disc SHRCM.G38197 (Text-fig. 10F).

Remarks. Dineley (1964) described a dorsal disc, NMC10373, from the Knoydart Formation, Nova Scotia, Canada, which he considered was sufficiently close to the specimens from the Anglo-Welsh region to call it *Traquairaspis symondsii*. However, until more Nova Scotian material is described, it is unjustifiable to consider that this specimen belongs to *P. symondsii*, and it is probably best referred to as *Phialaspis* sp.

Genus TOOMBSASPIS gen. nov.

Etymology. In remembrance of the late Mr H. A. Toombs, and *aspis*, Greek, shield.

Type species. Phialaspis pococki White, 1946

Other species assigned. Toombsaspis sabrinae (White, 1946)

Diagnosis. Small phialaspidids with lateral keels. Low dorsal vane. Ventral, longitudinal cyclomoriform units against each lateral side of ventral, smooth central area. Ornament of stellated, equilateral and elongated tubercles divided by fine ridges. Ventral disc tubercles elongated on sides, in stacked V-shapes at back.

Toombsaspis pococki (White, 1946)

Plate 5, fig. 1; Text-figs 1, 11, 14c–g, 15h; Table 2

1946 *Phialaspis pococki* White, pp. 217–229, pl. 12, fig. 1; figs 1, 3–8, 12–19, 22–27, 31–35, 39, 40–44, 55.

1948 *Traquairaspis pococki* (White); White and Toombs, p. 55, pl. 7, fig. 1.

Holotype. BMNH24511 dorsal disc.

Horizon and localities. Upper Silurian/Lower Devonian, Upper Downton Group. The Lower Old Red Sandstone of the Anglo-Welsh region (Text-fig. 1).

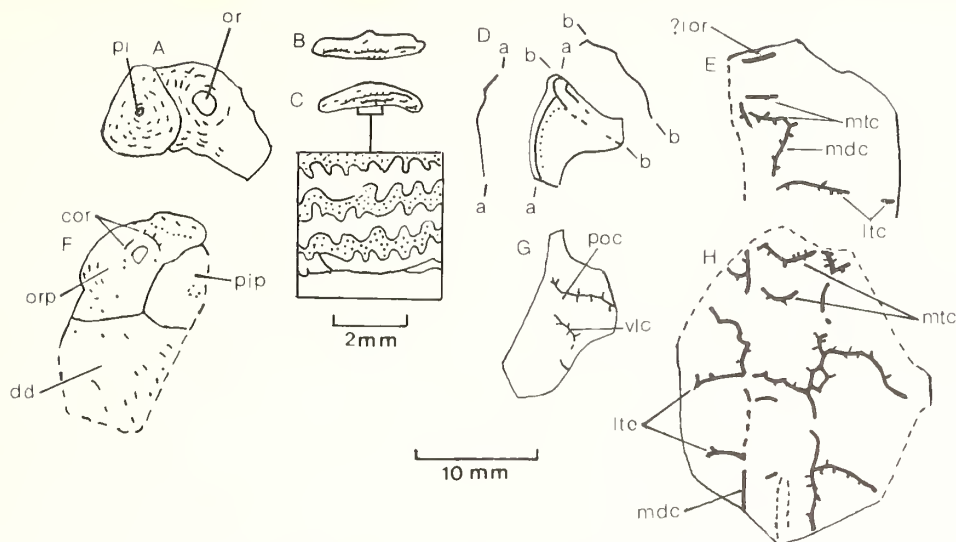
TABLE 2. Maximum dimensions of *Toombsaspis pococki* plates in millimetres. Abbreviation: pop, post-oral process.

	Range			Average		
	Length	Width	Ratio of width to length	Length	Width	Ratio of width to length
Dorsal discs	22–31	22–29	0.73–1.00	28	25	0.89
Orbital plates	11–13	7	0.53–0.63	12	7	0.58
Pineal plates	5–7	6–7	1.00–1.20	6	6	1.00
Rostrums	2	9	4.5			
Branchio-cornualls	25–29	6–7	0.24	27	6.5	0.24
Ventral discs	32–39	18–25	0.53–0.69	35	22	0.63
Lateral plates + pop	8	7	0.87			
Lateral plates – pop	14	7	0.50			
	Curvital dimensions					
Dorsal discs	22–31	24–31	0.89–1.09	28	27	0.96
Ventral discs	33–40	24–30	0.68–0.80	36	28	0.77

Referred material. Specimens housed in the BMNH (especially BMNH24751 and BMNH24568–9) and BU (especially BU2096–2102).

Diagnosis. Dorsal and ventral discs approximately evenly vaulted. Dorsal vane small with one cyclomoriform unit, dorsal median keel with two. Rostrum short. Dorsal disc tubercles long on units, equilateral on periphery.

Description. Internal impressions marking the edges of cyclomoriform units are not usually found, although White (1946) observed internal impressions in the dorsal disc BMNH24512, which he considered were left by sensory canals. These appear to resemble the internal impressions marking the edges of units in the dorsal discs of *P. symondsi*.



TEXT-FIG. 11. *Toombsaspis pococki* (White). A, pineal plate fused to orbital plate, BMNH24568-9. B, dorsal view of rostral plate, BMNH24751. C, ditto, anterior view, with detail of tip ornamentation. D, right lateral plate, a-a, b-b, lines of cross section, BU2097. E, internal view of left anterior side of dorsal disc showing sensory canals, BU2100a. F, fragmentary headshield, showing left orbital plate, and part of pineal plate and dorsal disc, BU2098. G, right lateral plate showing sensory canal system, BU481b. H, internal view of fragmentary dorsal disc showing sensory canals, BU2101. Abbreviations: cor, circum-orbital sensory canal; dd, dorsal disc; ?ior, possible inter-orbital sensory canal; ltc, lateral transverse sensory commissures; mdc, medial dorsal longitudinal sensory canal; mtc, medial transverse sensory commissures; or, orbital opening; orp, orbital plate; pi, pineal opening; pip, pineal plate; poc, post-oral sensory canal; vlc, ventral longitudinal sensory canal.

The dorsal disc is similar in shape to that of *P. symondsii* and two longitudinal rows of cyclomoriform units are found on each lateral side. The dorsal vane ranges from 2 to 3 mm in height and 6 to 9 mm in length.

The orbital plate (Text-fig. 11A,F), which is more gently curved than that of *P. symondsii*, is approximately ovate to diamond shaped. The orbital opening ranges from 1 to 1.5 mm, in diameter.

The pineal plate (Text-fig. 11A) is triangular in shape, with the greatest width at the posterior end. The pineal organ is centrally placed and penetrates the surface of the plate. The ornament on both the pineal and orbital plates is cyclomoriform, encircling the openings. BU2098 (Pl. 5, fig. 1; Text-fig. 11F) is a fragment of a dorsal headshield showing plate fusion between the dorsal disc, left orbital plate and pineal plate. The pineal organ can only be seen as an internal impression on the counterpart. The orbital plate forms a ridge at its anterior edge, where it would have met the rostrum. BMNH24568-9 (Text-fig. 11A), identified by White (1946) as an orbital plate, is a pineal plate fused to a right orbital plate.

The rostrum BMNH24751 (Text-fig. 11B,C) was originally considered to have been a pineal plate (White 1946). It is proportionally much shorter than the immature *P. symondsii* rostrum, and more closely resembles that of *?Traquairaspis adunata* Dineley and Loeffler, 1976, with elongated tubercles running in rows across its anterior end and no prominent anterior apex.

The branchio-cornual plates (White 1946) are proportionally flatter and less massive than those of *P. symondsii* and, with no lateral vanes, their shape is generally closer to those of *Traquairaspis campbelli*. The branchial opening is about 2.5 mm long \times 1.5 mm wide. It faces dorso-laterally and is located at about three-fifths along the length of the plate from the front. The tubercles on the dorsal side tend to be elongate, and a row of cyclomoriform units overlies the lateral dorsal longitudinal sensory canal.

Excluding the smooth central area, the ventral disc (White 1946) is more vaulted than that of *P. symondsii* and, on average it has proportionally larger central area. This ranges from 24-27 mm in length to 10 to 12 mm in width. There is a well-defined row of cyclomoriform units resting against each side of the central area, with no intervening rows of ornamented growth.

Although much smaller, the lateral plates (Text-fig. 11D,G) closely resemble those of *P. symondsii*. They

usually have an attached post-oral process. Nevertheless, White (1946) illustrated a specimen, BU4816, with the post-oral process apparently missing (Text-fig. 11G). White also described a possible anterior lateral plate BMNH24788 and a ridge scale BMNH24759. These appear to be similar to their corresponding parts in *P. symondsi*.

The sensory canal system (Text-figs 11E,F,H and 14) is incompletely known, but appears to be arranged similarly to that of *P. symondsi*. However, the dorsal lateral transverse commissures are longer, and the inter-orbital canal may have extended into the anterior edge of the dorsal disc (Text-fig. 11E).

Remarks. *T. pococki*, which retains more in common with the earlier Traquairaspididae than *P. symondsi*, must be considered as a more primitive phialaspidid. The specimens of a traquairaspidiform from the Red Bay Series, Fraenkelryggen Formation, Spitsbergen, considered by Blicek (1983) as *Traquairaspis* cf. *pococki*, are considerably larger than comparable Anglo-Welsh *T. pococki* specimens, and are provisionally assigned to Traquairaspidiform fam., gen. et sp. indet.

Toombsaspis sabrinae (White, 1946)

1946 *Phialaspis pococki* var. *sabrinae* White, pp. 217–229, pl. 12, figs 2–4; figs 2, 9–11, 20, 21, 28–30, 56.

Holotype. S4, dorsal disc (White 1946).

Type horizon and locality. Upper Silurian/Lower Devonian, Upper Downton Group, Lower Old Red Sandstone, Sharpness, Gloucestershire, England (Text-fig. 1).

Diagnosis. Dorsal disc approximately 30 mm long with equilateral tubercles. Dorsal vane large with long median tubercle, continuous with dorsal keel.

Genus MUNCHOASPIS nov.

Etymology. After Lake Muncho, British Columbia, and *aspis*, Greek, shield.

Type species. *Traquairaspis denisoni* Dineley, 1964.

Diagnosis. Dorsal disc approximately ovate, attaining length of 100 mm, with median keel, no dorsal vane, longitudinal carina on each lateral side marking the change in vaulting and double cyclomoriform whorl on the anterior. Ornament in long fine ridges which run parallel to the anterior and lateral edges.

Munchoaspis denisoni (Dineley, 1964) comb. nov.

1964 *Traquairaspis denisoni* Dineley, pp. 211–215, pl. 38; text-figs 1–4.

Holotype. NMC10371, dorsal disc.

Type horizon and locality. Silurian, Ludlow/Pridoli, North West of Lake Muncho, British Columbia, Canada.

Diagnosis. As for genus, the only known species.

Remarks. Dineley (1964) described several incomplete ventral discs from Canada, which he considered were indistinguishable in outline from the British ones. The smooth ventral central region, surrounded by a gently sloping ornamented brim with peripheral adult growth impressions, is a further typical phialaspidid characteristic. The early occurrence of this species would appear to strengthen Dineley and Loeffler's (1976) claim for a traquairaspidiform evolutionary centre in Western and Arctic Canada.

Family TRAQUAIRASPIDIDAE Kiaer, 1932

Type genus. *Traquairaspis* Kiaer, 1932

Other genus assigned. *Rimasventeraspis* nom. nov.

Diagnosis. Ventral disc with narrow ornamented margins, steep lateral sides each with a longitudinal row of elongated tubercles surrounded by cyclomorior fine ridges. The posterior edge sometimes medially notched. Large ventral central area extending to posterior edge, either totally smooth, partly subdivided, or with irregular dentine ridges, and on the anterior half, ventral medial commissures and post-oral sensory canals.

Genus TRAQUAIRASPIS Kiaer, 1932

Type species. *Cyathaspis campbelli* Traquair, 1913

Diagnosis. Dorsal disc not fused to adjacent plates, ornamented with twelve or more, alternating, longitudinally running rows of small cyclomorior units. Low dorsal, postero-medial keel. The branchio-cornual plates narrowly keeled behind the enclosed branchial openings. Two distinct types of ventral discs; type 1- smooth central area extending the length of plate (White 1946), type 2- posterior margin deeply notched, median region with a maze of dentine ridged units (Tarlo 1960).

Traquairaspis campbelli (Traquair, 1913)

Text-fig. 12; Table 3

- 1911 *Cyathaspis* n.sp. Traquair in Campbell, p. 66.
 1913 *Cyathaspis campbelli* Traquair in Campbell, p. 932.
 1932 *Traquairaspis campbelli* (Traquair); Kiaer, pp. 25–26, pl. 11.
 1946 *Phialaspis pococki* subsp. *cowiensis* White, p. 239, figs 36–38.

TABLE 3. Maximum dimensions of *Traquairaspis campbelli* plates in millimetres.

	Average		Ratio of width to length
	Length	Width	
Dorsal disc	39	27	0.69
Branchio-cornual	39	11	0.28
Ventral disc type 1	44	27	0.61
Ventral disc type 2	49	22	0.44

Holotype. RSM1960. 14. 1.

Horizon and locality. Upper Silurian, Pridoli, Stonehaven, Kincardineshire, Scotland.

Referred material. Specimens in the BMNH.

Diagnosis. As for genus.

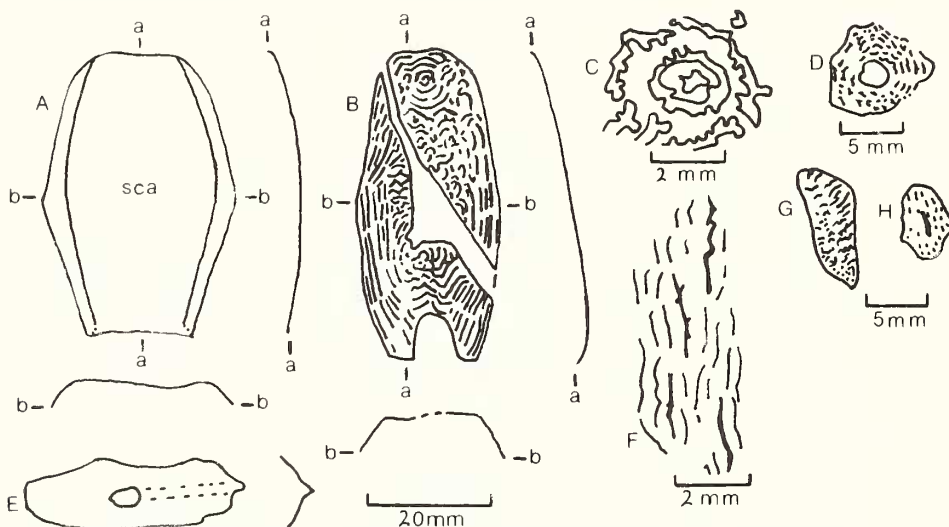
Description. The dorsal disc is four-sided, vaulted posteriorly, flattened anteriorly, its lateral and posterior edges are gently convex, its anterior edge is indented, and it has slightly raised tubercles at the posterior edge.

A broken plate (Text-fig. 12b) located on the slab BMNH27388, measures 8 × 7 mm, and is perforated

medially by a 2 mm wide foramen. Although Dineley and Loeffler (1976) have described distinctive pineal foramina in several Canadian traquairaspiforms, the large size of the opening shows that this specimen probably represents an orbital plate.

The branchial opening is about 4 mm long \times 3 mm wide, postero-laterally facing, and located at about two-fifths along the length, from the front of the branchio-cornual plate (Text-fig. 12E). Fine elongated tubercles run longitudinally behind, and curve across the plate in front of, the branchial opening.

Although the two types of ventral disc could prove to indicate two distinct species, they have identical lateral ornamentation and proportional overlap (Table 3; Text-fig. 12A,B). Also, problems occur with categorizing the other plates into two types. This may indicate that the two types of ventral discs are dimorphic, possibly sexual, examples of the same species. White (1946) showed the segmented longitudinal sensory canals running in association with the longitudinal row of tubercles on each lateral side of ventral disc type 1. Pores show the



TEXT-FIG. 12. *Traquairaspis campbelli* (Traquair). A, ventral disc type 1, a-a, b-b, lines of cross section, BMNH37379, B, ventral disc type 2, a-a, b-b, lines of cross section, BMNH27037. C, ditto, detail of ornamentation on central area. D, fragmentary orbital plate, p.27388. E, branchio-cornual plate, plus cross section, BMNH43544. F, detail of dorsal disc ornamentation, BMNH43523. G, flank scale, on BMNH43525. H, ridge scale, on BMNH43525. Abbreviation: sca, smooth central area.

presence of post-oral canals running on to the anterior half of the smooth central area. These also show the positions of probable ventral medial sensory commissures.

On the slab BMNH43525, there are scales of two types. The ridge scales (Text-fig. 12H) lack the pronounced spine or spinal process of phialaspids, and instead they have a medially placed elongated tubercle. The flank scales (Text-fig. 12G) are very wide compared to those of *P. symondsii*. The most complete ridge scale measures 6 mm long \times 4 mm wide and the most complete flank scale measures 5 mm long \times 10 mm wide.

Remarks. The morphological similarity and contemporaneity with the Canadian traquairaspiforms supports Dineley and Loeffler's (1976) assignment of its part of Scotland to the North American Silurian continent. This arrangement is shown by Scotese *et al.* (1985) on their Silurian and Devonian base maps.

Genus RIMASVENTERASPIS nom. nov.

Etymology. *Rimas venter*, Latin, fissured belly, and *aspis*, Greek, shield.

Type species. ?*Traquairaspis angusta* Denison, 1963.

Remarks. The previous generic name is pre-occupied (*Yukonaspis* Kobayshi, 1936).

Diagnosis. Ventral disc; 80–85 mm long \times 35.5 mm wide, with medially notched posterior edge. Ventral smooth central area covers nearly all the disc, is partly subdivided into units which grade into tubercles on antero-lateral edges. Ornament of stellated tubercles became elongated and divided by fine ridges on lateral sides.

Rimasventeraspis angusta (Denison, 1963)

1963 ?*Traquairaspis angusta* Denison, pp. 132–135, figs 78 and 79.

1964 *Yukonaspis angusta* (Denison); Obruchev, p. 63; Stensiö, p. 364, fig. 123 A.

Holotype. PU17388, ventral disc.

Type horizon and locality. Silurian, Ludlow/Pridoli, Beaver River, South-eastern Yukon, Canada.

Diagnosis. As for genus, the only known species.

Remarks. A ventral disc fragment described by Dineley and Loeffler (1976) as ‘*Traquairaspididae* indet. Type 1’, from the Pridoli of the Delorme Formation, Mackenzie, Canada, may be conspecific with, or closely related to, *R. angusta*.

Discussion. The Traquairaspidinae are readily distinguished from the Phialaspidinae, by a ventral disc with steep sides and a large ventral central region extending to the posterior edge. The ornamentation of small cyclomoriform units suggests a more scale-like dermal arrangement than is found on the phialaspidinids. This, together with the wide flank scales and the absence of a specific pattern of adult growth, would suggest a more primitive condition, in comparison with undifferentiated very scale-like ornamentation and extremely wide, spindly scales of the Ordovician heterostracon *Arandaspis* (Ritchie and Gilbert-Tomlinson 1977).

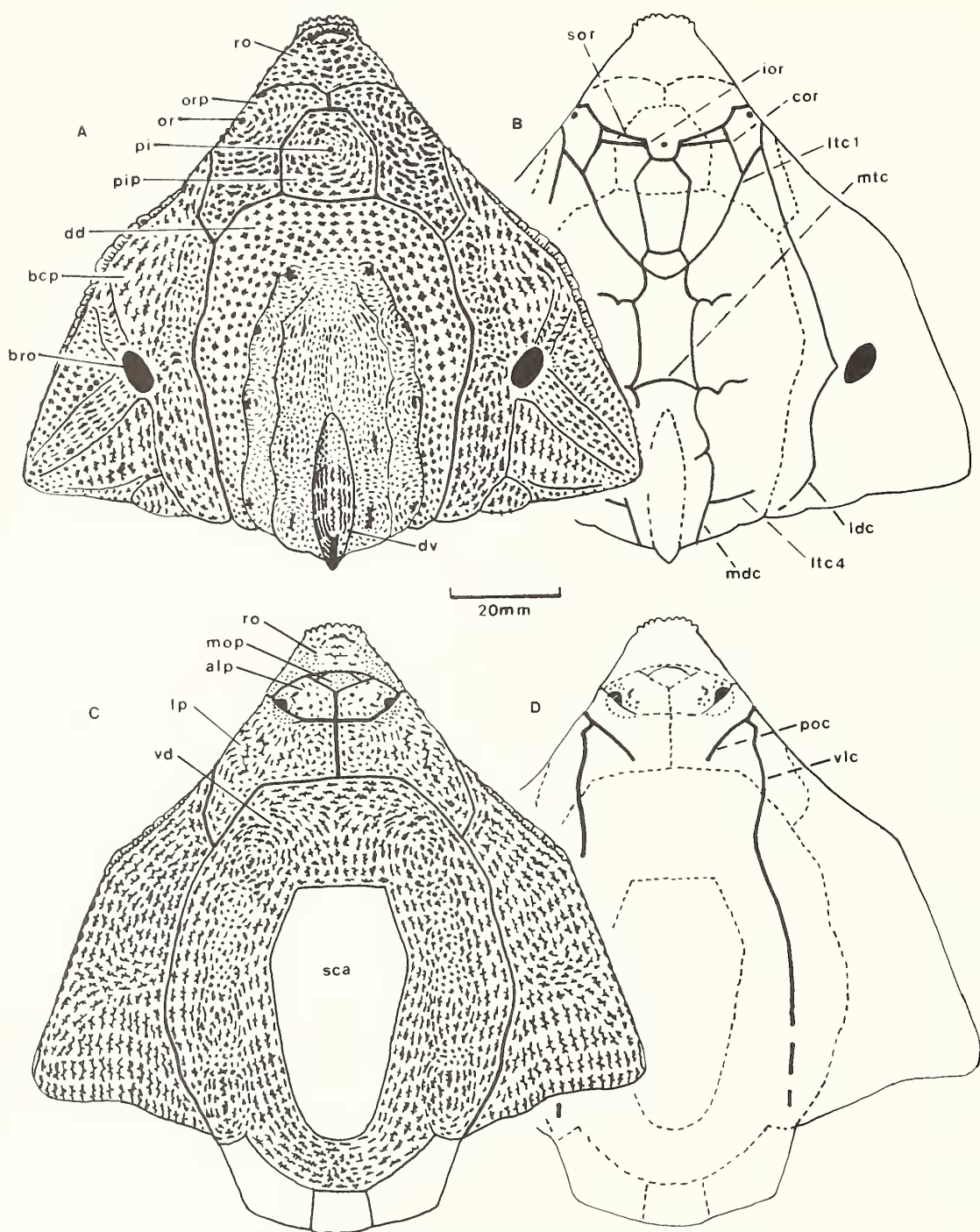
RESTORATION OF PHIALASPIDID CARAPACES

The reconstructions of phialaspidid carapaces (Text-figs 13 and 14) are based upon average measurements (Tables 1 and 2) because of the large proportional range of individual plates, in particular in *P. symondsi*. They have been based upon specimens showing plate fusion, the matching of similarly shaped and sized edges, the similarity of alignment and type of ornament, the matching of the sensory canal system and plate orientation in other heterostracans. Impressions were taken of individual specimens of each component plate, and models were made for both *P. symondsi* and *T. pococki*. This has shown that the plate arrangements in both genera were identical, with the exception of the junction of orbital plates of *P. symondsi* between the rostrum and the pineal plate. In certain regions one edge is often more strongly angled than its corresponding plate margin, suggesting (White 1946) the former presence of small areas of connective tissue.

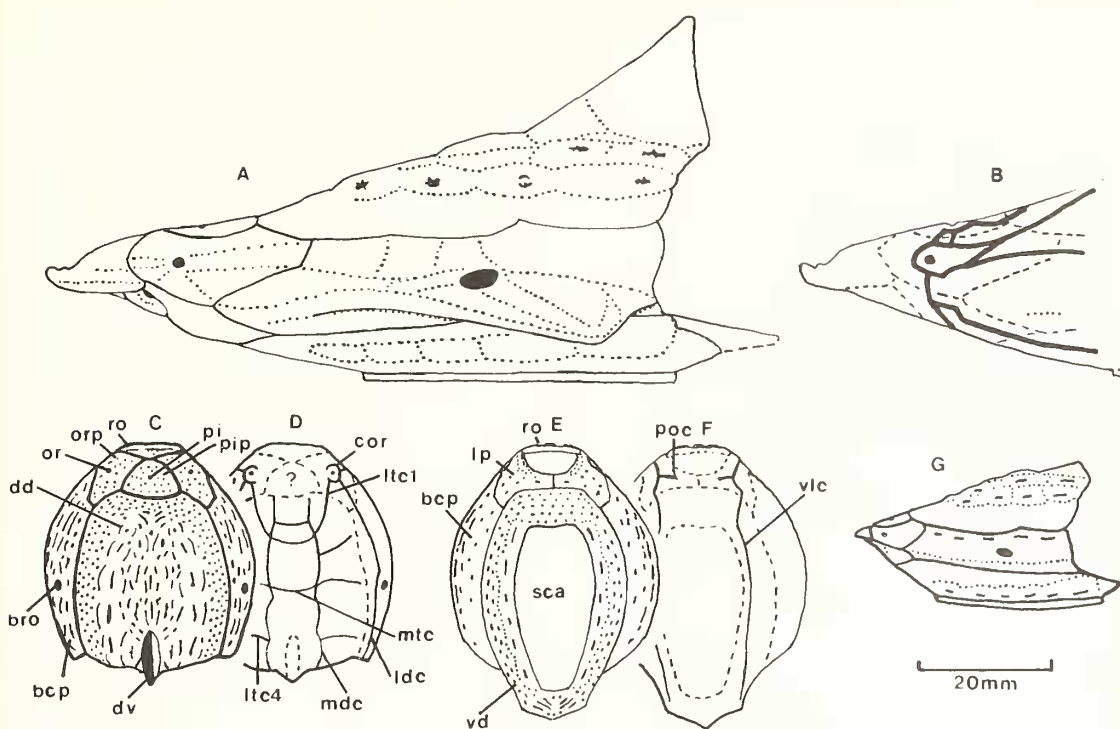
INTERNAL ANATOMY

Impressions of internal organs on the inside of the plates tend to be obscured by impressions of plate growth. Partly because of this, with the exception of the pineal organ, there are no distinguishable impressions of the brain, the semicircular canals, or nasal sacs.

Impressions of the vascular system. The impressions of vessels and possibly nerve fibres, in the basal laminated layer of the exoskeleton, can be seen on many of the specimens of *P. symondsi* from Devil’s Hole. These are clearest where radiating from the centres on the interiors of the ventral discs (Text-fig. 10c). The impressions are too incomplete to observe their general ramification, but, at frequent intervals along their lengths, branches leave at right-angles to run through the basal laminated layer into the exoskeleton. As Janvier and Blicek (1979) have observed, these are usually seen as small foramina in the basal laminated layer in heterostracans.



TEXT-FIG. 13. *Phialaspis symondsii* (Lankester), reconstruction of headshield. A,B, dorsal view showing ornamentation and sensory canal system. C,D, ventral view showing ornamentation and sensory canal system. Abbreviations: alp, anterior lateral plate; bcp, branchio-cornual plate; bro, branchial opening; cor, circum-orbital sensory canal; dd, dorsal disc; dv, dorsal vane; ior, inter-orbital sensory canal; ldc, lateral dorsal longitudinal sensory canal; lp, lateral plate; ltc, lateral transverse sensory commissure; mdc, medial dorsal longitudinal sensory canal; mop, median oral plate; mtc, medial transverse sensory commissure; or, orbit; orp, orbital plate; pi, pineal opening; pip, pineal plate; poc, post-oral sensory canal; ro, rostrum; sca, smooth central area; sor, supra-orbital sensory canal; vd, ventral disc; vlc, ventral longitudinal sensory canal.

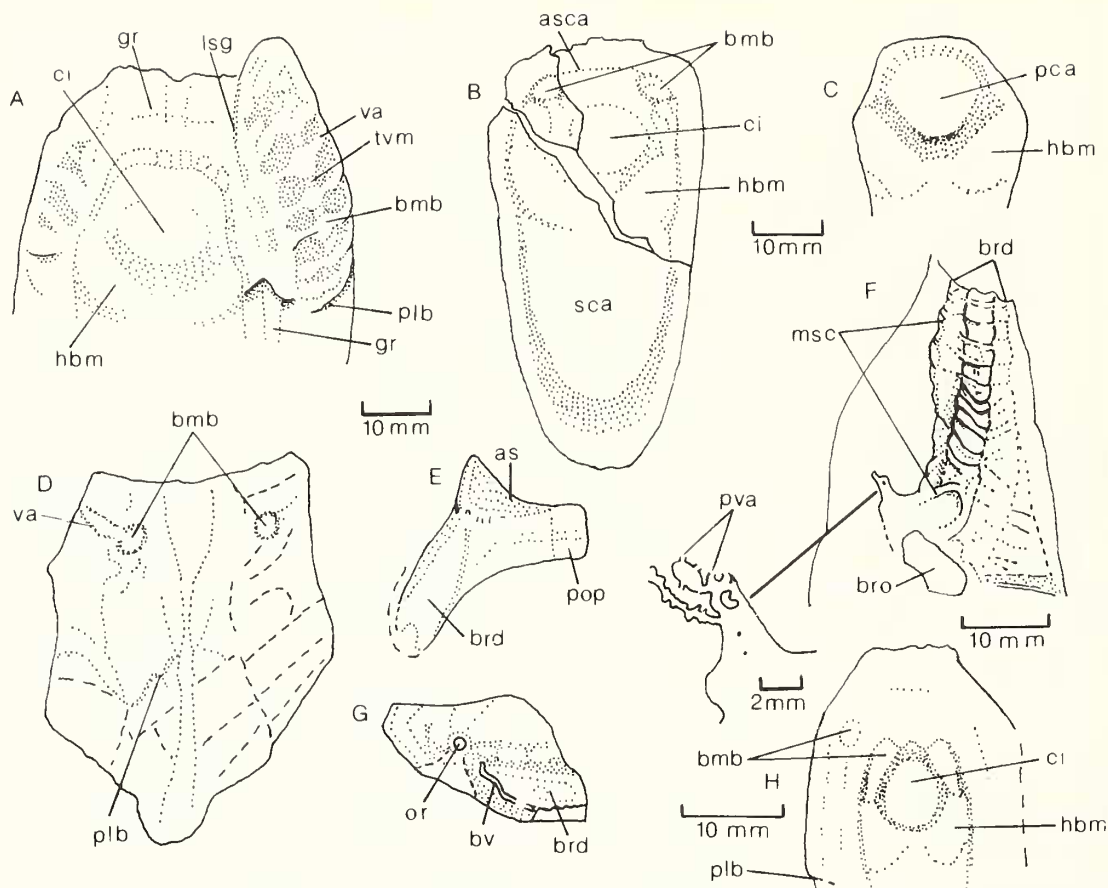


TEXT-FIG. 14. Reconstruction of headshields. A,B, *Phialaspis symondsii* (Lankester); A, lateral view; B, lateral view of anterior portion with sensory canal system. C-G, *Toombsaspis pococki* (White); C,D, dorsal view showing ornamentation and sensory canal system; E,F, ventral view showing ornamentation and sensory canal system; G, lateral view. (See Text-fig. 13 for symbols)

A cone-shaped structure (Text-fig. 15F) found only on the branchio-cornual plate, SHRCM.G08152/1, runs into the exoskeleton of the lateral keel, from near the branchial opening on the branchial duct. It is 6 mm long, 4 mm wide at its base, tapers to 1 mm wide at its tip, and lies at an antero-lateral angle of 50° from the branchial duct. Impressions of vessels adjoin it in places, in particular at the tip.

Branchial structures. The internal, paired and ovate impressions, running in longitudinal rows along heterostracan dorsal and ventral shields, are generally considered to have been made by gill pouches, as originally suggested by Woodward (1891). Stensiö (1958) interpreted longitudinal grooves on the ovate impressions as gill lamellae. Tarlo and Whiting (1965) considered that the paired impressions were made by head somites, which were used to pump the gills. In contrast, Janvier and Blicek (1979) considered that the cephalic somatic musculature was much reduced or absent in the Heterostraci, and its place filled by the branchial apparatus, and that the impressions they observed represented branchial and extrabranchial divisions of the gill pouches, visceral arches with attachment points to the exoskeleton, and an arrangement of nerves closely resembling those found on the branchial regions of the Osteostraci, and the ammocete larva.

White (1946) recognised paired branchial impressions on the anterior parts of a ventral disc of *T. campbelli*. Although he was uncertain about the 'lobes' originally found by Wills (1935), on the smooth, ventral central area of *P. symondsii*, he observed a pattern of rounded ridges on the external surface of that region, in the type specimen of '*Psammosteus anglicus*'. The ventral discs from Devil's Hole show that these impressions run around the shapes of three usually strong and commonly found internal impressions (Text-fig. 15A-C). The most anterior of these is medially



TEXT-FIG. 15. Internal impressions. A–G, *Phialaspis symondsii* (Lankester): A, anterior part of ventral disc showing branchial impressions, SHRCM.G3339; B, immature ventral disc showing branchial impressions, SHRCM.G3527A; C, internal impression of anterior part of ventral smooth central region, SHRCM.G08144; D, imperfect dorsal disc showing branchial impressions, SHRCM.G08144; E, internal view of lateral plate, SHRCM.G08173/2; F, internal view of branchio-cornual plate showing impressions on branchial duct, with detail of vascular structure, SHRCM.G08152/1. G, internal view of orbital plate, SHRCM.G3387. H, *Toombsaspis pococki* (White), anterior of ventral disc showing internal impressions, BU2099. Abbreviations: as, anterior side; asca, anterior edge of smooth central region; bmb, branchial muscle block; brd, branchial duct; bro, branchial opening; bv, blood vessel; ci, central impression; gr, growth ridge; hbm, hypobranchial muscles; lsg, groove for longitudinal sensory canal; msc, muscle scars; or, orbital opening; pca, pre-branchial central impression; plb, posterior limit of branchial region; pop, post-oral process; pva, points of vascular attachment; sca, smooth central area; tvn, transverse muscles; va, visceral arch.

EXPLANATION OF PLATE 6

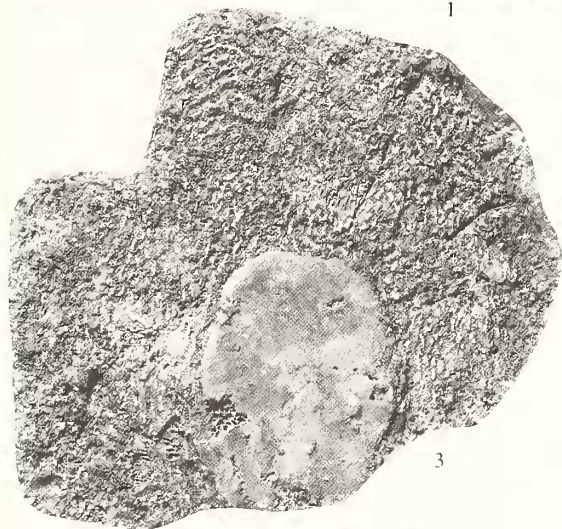
Figs 1–5. *Phialaspis symondsii* (Lankester), lower Devonian, Welsh Borderland. 1, SHRCM.G3339/1, anterior of internal mould of ventral disc, $\times 2$. 2, SHRCM.G08152/1, internal impression, detail of branchial duct, $\times 4$. 3–5, regions of injury on ventral discs; 3, SHRCM.G08168, external right anterior side of cast, $\times 1.5$; 4, SHRCM.G08195/1, anterior of internal mould, $\times 1.5$; 5, SHRCM.G3302/1, internal anterior of cast, $\times 1$.



1



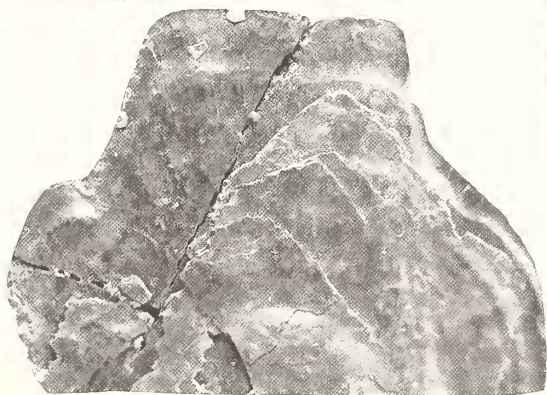
2



3



5



4

placed and rounded, with an average diameter of 10 mm. At its posterior end, the other impressions form a pair, join medially and fan out antero-laterally on each side, to define the antero-lateral edges of the smooth central region. The average measurements of each of these impressions are about 14 mm long \times 7 mm wide.

Branchial impressions can be best seen on the internal mould of the ventral disc, SHRCM.G3339 (Pl. 6, fig. 1; Text-fig. 15A) and these run from the three centrally placed impressions to the antero-lateral edges of the disc. Their posterior edges are clearly defined, and Wills (1935) described these in his specimens, as grooves of indeterminate origin. Lines of beaded, 2 mm wide and raised impressions, divided by lines of pits, are contained on each side within a fan-shaped area. Seven or possibly eight rows are on the left side. On an immature ventral disc SHRCM.G08192 (Text-fig. 15B) the beaded impressions are found closer beneath the internally flattened, antero-lateral corners of the smooth central area, and the two sides are closer together. This resembles the arrangement on the ventral disc of *T. pococki* (Text-fig. 15H). In the dorsal discs, only the distorted specimen SHRCM.G08194 (Text-fig. 15D), shows any branchial impressions, and these are incomplete, but are of the same beaded type as those on the ventral discs.

A row of Y- or U-shaped impressions, running along the dorsal side of the heterostracan branchial duct, and corresponding to the more medially placed branchial impressions, have been interpreted as part of the gill pouches (Kiaer 1930; Kiaer and Heintz 1935; Wills 1935), as impressions marking the positions of branchial pouch openings (Watson 1954; Stensiö 1958, 1964; Tarlo and Whiting 1965; Jarvik 1980), or of visceral arches (Halstead 1982).

The branchial duct in *P. symondsi* can be detected running longitudinally, from below the orbit and the deepest part of the lateral plate, to the branchial opening (Text-fig. 15E,G,F). It is seen most clearly on the branchio-cornual plate SHRCM.G08152/1 (Pl. 6, fig. 2; Text-fig. 15F), where well-defined impressions run transverse across it, along the length of its dorsal side, and most strongly near the branchial opening.

With the possible exception of a large blood vessel on the branchial duct of the orbital plate SHRCM.G3387 (Text-fig. 15G), no obvious impressions of branchial blood vessels or nerves have been detected.

The rows of beaded and depressed impressions undoubtedly represent the positions of visceral arches. The incompleteness and inconsistency of the impressions appears to indicate that the main respiratory movements were endoskeletal, and were mostly made by the branchial region when it was fully expanded. The flexibility and elasticity of the cartilaginous visceral arches would have been an important factor in the extension and contraction of the branchial regions. This explains the rows of beaded impressions, which would represent the positions of branchial muscle plates overlying the visceral arches, and transverse muscles running in between. The large paired impressions, usually found under the smooth ventral central area, have all the appearance of two large hypobranchial muscles, which would have served to raise and lower the branchial regions.

The impressions on the branchial duct of *P. symondsi* could hardly be described as Y- or U-shaped, but rather as bands joining the more medial branchial regions, and swathing the branchial duct. It is unlikely that impressions left by the extrabranchial atria would be found on the lateral branchial region, since they would have been positioned away from the exoskeleton. The impressions in *P. symondsi* appear more like muscle bands, which would have strengthened the internally hollowed and bulky lateral exoskeleton, and could have forced water out through each branchial opening by longitudinal waves of compression, to aid in steering and in controlling pitch and roll.

Janvier and Lund (1983) argued that hypobranchial somatic musculature, found on the myxinoids, anaspids, and to a lesser extent on the lampreys, mobilized the anterior parts of the body, compensating for the lack of paired fins. The same was possible for a juvenile *P. symondsi* at a stage prior to plate growth, as was suggested for the Heterostraci by Tarlo and Whiting (1965). These same muscular contractions could have been used by the adults, to control jet-aided steering and balance.

It seems odd that the Heterostraci did not need paired fins; it seems likely that they had evolved

their own substitute. *P. symondsi*, with its streamlined shape, large dorsal and lateral vanes, which indicate an active existence, and its obvious ability to frequent narrow meandering channels, must have manoeuvred more efficiently than is supposed for the Heterostraci, despite its rigid carapace. Water under pressure, forced out of the branchial opening on one side, would push the same side downwards, causing the animal to roll. If this coincided with a yaw in the same direction, the animal would bank, using its wide undersurface to effect a turn. If water was expelled with force from both branchial openings at the same time this would raise the anterior end, which could direct the animal upwards, and slow it down, or stop its forward motion, using the underside as a brake. It seems likely that this proposed method of jet-aided steering could have originally developed as a method of expelling debris from the large and enclosed branchial regions.

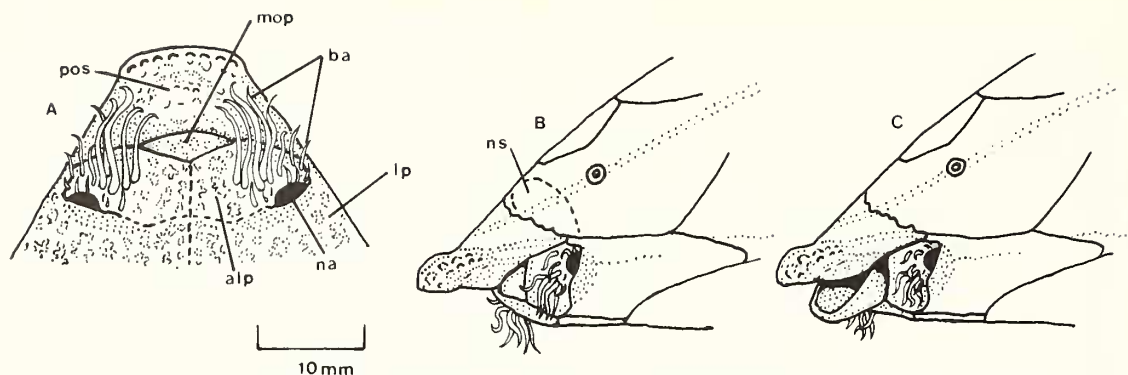
Jarvik (1980) suggested that water expelled through the branchial openings of the pteraspidiiforms would have aided the forward movement of the animals to some extent, as is known for modern actinopterygians. As many heterostracans are streamlined, especially so with certain large and advanced pteraspidiiforms, it must be assumed that efficient manoeuvrable free-swimming must have been achieved, despite the inflexibility of the carapace. As the branchial openings on most species are directed posteriorly, it is probable that forward movements were jet-aided. The independent expulsion of water to aid in steering in these animals would be less efficient, and would have worked in the opposite way, to the method suggested for *P. symondsi*.

Oral and olfactory apparatus and feeding methods. It has been generally accepted that two circular impressions found internally on the anterior edge of the heterostracan dorsal headshield indicate the position of nasal sacs, as first described by Jaekel (1903). Rostral spaces, medially divided to various degrees, have been found in certain pteraspidiiforms (Stensiö 1927, 1932a; Heintz 1962; Denison 1964, 1970) and in the cyathaspidid *Torpedaspis* (Broad and Dineley 1973). With the exception of Stensiö (1958, 1964, 1968), who considered that the spaces were filled with cartilage, it has been generally agreed that they would have housed the anterior part of the nasal sacs. Although it has been considered that in some heterostracans the olfactory organ or organs opened into the buccal cavity (White 1935), notches on the anterior edge of the dorsal armour have been described as external nares (Kiaer and Heintz 1932; Watson 1954; Novitskaya 1975). Paired grooves on the rostral under surface of certain pteraspidiiforms have been described as olfactory grooves (Zych 1931; Tarlo 1961), or as impressions indicating the position of tentacles (Stensiö 1958; Janvier 1974; Jarvik 1980).

Stensiö (1927, 1958, 1964) was the first to suggest a close affinity between the Myxinoidea and the Heterostraci. In order to do this, he considered that the Heterostraci had a palatosubnasal lamina with 'upper labial plates' against which the oral plates worked, separating the oral cavity from a single medially-placed olfactory organ duct and opening. As no fossil evidence of 'upper labial plates' has been found, Denison (1960), White (1961), Tarlo (1961), Heintz (1962), Halstead (1973), and Novitskaya (1975), disagreed with Stensiö's suggested parts. Stensiö was supported by Jarvik (1980) and by Janvier (1974) who later rejected a close relationship between the two classes, mainly because the Myxinoidea have a single semicircular canal and that the Heterostraci had two (Janvier and Blicek 1979), although they still maintained that the Heterostraci had a 'palatosubnasal lamina', and favoured for most Heterostraci, a medial position for a single olfactory opening, duct and organ. In contrast, Halstead (1973) and Novitskaya (1975) considered that there were two olfactory organs, as in gnathostomes.

The small size and the positions of phialaspidid orbital openings suggest a limited range of vision. Therefore, there must have been a heavy reliance upon well-developed olfactory organs, and possible tactile taste organs, to detect food.

In *P. symondsi*, the folded and contorted under-surface of the back of the rostrum indicates a likely continuation of the external skin that covered the ventral pre-oral surface, and an attachment area for the soft dorsal parts of the mouth. The absence of rostral spaces, the large median oral plate which would have filled the oral cavity medially, plus the likely soft supportive and muscular structures of the oral region, suggest the anterior absence of a palatosubnasal lamina, and a more



TEXT-FIG. 16. *Phialaspis symondsii* (Lankester). A, ventral view of oral region. B, anterior part of head with mouth closed. C, ditto, with mouth open. Abbreviations: alp, anterior lateral plate; ba, barbels; lp, lateral plate; mop, median oral plate; na, narial opening; ns, nasal sac; pos, pre-oral surface.

posteriorly placed olfactory complex, than is accepted on the pteraspidiiforms. This indicates lateral positions for possible inhalant openings. It seems that the raised notch on the anterior lateral plate represents an inhalant opening, indicating that *P. symondsii* had paired inhalant olfactory ducts. The foramina surrounding the raised notch might suggest the positions of tactile and possible taste organs. These could possibly be extensions of the olfactory apparatus, as in the myxinoids (Janvier 1974).

The raised notch and foramina may have served to house a large tentacle on each side of the oral cavity. The abrasions on the sides of the median oral plate appear to have been caused by friction against the overlapping anterior lateral plates, indicating that the latter were hinged at their posterior edges, and would have swung open as the median oral plate was extruded. This action, taking into account the shape of the front of the lateral plates, could have been restrained by such tactile organs.

It seems likely that the nasal sacs would have been separated, and have rested under the anterior of the orbital plates. A more medial position for a single olfactory organ would have meant that it had to rest under the telencephalon, which would have involved excessive cranial flexure and where there would have been insufficient room.

Georgieva *et al.* (1979) considered the 'sensory buds' on the barbels of *Myxine glutinosa* resembled the taste buds of the gnathostomes, and Baatrup (1983) described sensory buds in larval lampreys akin to the taste buds of other vertebrates. Therefore, it is feasible that *P. symondsii* may have possessed similar structures, in particular on its tactile organs.

Various suggestions have been made about the oral workings of Heterostraci, particularly the pteraspidiiforms and certain cyathaspidiiforms. Kiaer (1928) considered that the oral plates bit against the maxillary brim, on the ventral margin of the rostral region. Stensiö (1932) and Janvier (1974) thought that they worked in a myxinoid-like manner. White (1935) considered that the oral plates were connected together by the epidermis, and would have moved down and forwards, to form a scoop or shovel, and Denison (1961) further suggested that the protrusible mouth could have selected and picked up food, including small invertebrates. This could have been aided by inhalant respiratory currents. Dineley and Loeffler (1976) described a large plate in the oral region of *Poraspis cf. polaris*, which they interpreted as a large single oral plate used as a scoop.

P. symondsii had far fewer oral components than the pteraspidiiforms, and it is inconceivable to imagine its large median oral plate retracting, *Myxine*-fashion, into its gullet. The shape of the median oral plate indicates that it would have worked in the way that White (1935) and Denison (1961) described for the pteraspidiiforms. The elongate and convex area on its inner side indicates an attachment area for protractor and retractor muscles, and this suggests that the median oral plate could have, if needed, worked rapidly, snapping shut with force. The smooth edges show that

it had no grasping or cutting facilities, although it may have worked against the maxillary flange and pre-oral surface. The size of the oral cavity, surrounded by rigid lateral plates, limited the size of food engulfed. Nevertheless, the oral region of *P. symondsi* has all the appearance of working like an efficient trap, with its scooping median oral plate embraced by anterior lateral plates.

The shape of *P. symondsi*, albeit constricted by an inflexible carapace, has the lines of an active feeder, rather than a sluggish animal swallowing mud and filtering organic substances, as has often been supposed for the Heterostraci (Halstead 1985). The apparent lack of wear on the tip of the median oral plate appears to substantiate this. The small size and structure of the oral region would have prevented total filter feeding in open water. As White (1946) suggested for *Phialaspis*, the smooth ventral central area could have been used as a sliding plane and fulcrum, while the animal wriggled across the surface of the substrate. Taking the dorso-ventrally flattened, and anteriorly heavy, carapace into consideration, plus occasional abrasion observed on the anterior part of the ventral discs and undersurface of the branchio-cornual plates, the crenulated tip of the rostrum, and the ventral position of the oral region, it seems likely that *P. symondsi* was mainly a benthic feeder, rooting in the substrate. This, plus its common and wide occurrence, indicates that it was not a highly specialized feeder, but more of an opportunist, feeding on a wide range of animal and vegetable matter, both dead and alive. Its small mouth rules out any extensive predatory role, but it appears well-equipped to snap up small animals, which it would have disturbed out of the substrate. *T. pococki* had a more evenly vaulted cephalothorax and a short rostrum. Its oral region was more terminal in position (Text-fig. 14E-G), which indicates that it may have fed not so much within the substrate, but more on or possibly somewhat above its surface.

GROWTH AND ONTOGENY

Despite divergent views on heterostracan exoskeletal growth, evidence is patchy. From studies on elasmobranch scales, Ørvig (1951) developed the Lepidomorial Theory, which Stensiö (1958) used to interpret heterostracan exoskeletal growth. This, he considered, was achieved in two ways: (1) cyclomorial growth, in which peripheral concentric growth took place around an initial primordium, and (2) synchronomorial growth, in which calcification was achieved simultaneously, to produce a completed part of the carapace. This was mainly based on the assumption that, once a part of the carapace mineralized, it remained unchanged, and that the mode of growth could be deduced from the form of dentine patterning. However, Dineley and Loeffler (1976) discovered concentric growth impressions in association with synchronomorial dentine patterns in certain cyathaspidiform shields. From this, they argued that the Lepidomorial Theory was not applicable to heterostracan exoskeletal growth, and was only useful to describe cyclomoriform and synchronomoriform ornamental pattern.

An example of phylogenetic heterostracan exoskeletal growth can now be demonstrated, since Elliott (1984) has shown that the pteraspidiforms were derived from the cyathaspidiforms. The superficial layer formed prior to the underlying layers in the cyathaspid (Denison 1964), and during early ontogeny in the pteraspidiforms (Denison 1973; White 1973). The cyathaspidiform shield did not form until the animal had achieved its definitive size (Denison 1964; Dineley and Loeffler 1976), whereas the pteraspidiform shield grew as separate peripheral plates, which fused together at maturity (Heintz 1938; White 1958). This latter process was progressively delayed in later forms (White 1958).

As Dineley and Loeffler (1976) argued, it is likely that the earliest traquairaspidiforms had an undivided dorsal shield, although how this was formed is open to speculation. Nevertheless, to aid in synchronous growth between the animal and its exoskeleton, later forms attained a mode of plate division parallel to the pteraspidiforms.

The orbital, pineal and lateral plates mainly grew cyclomorally by peripheral additions. Much the same could be said about the regions of mature growth in the other major plates. Nevertheless, it would appear likely that some plate remodelling may have been required for fusions and to sustain the proportional vaulting and matching of peripheral plate contacts. Similar speculations

have been made about resorption and regrowth in the pteraspidiiforms (Halstead 1969; Denison 1973; White 1973), although it has never been demonstrated. However, Tarlo (1965) has shown that certain heterostracans were capable of resorption and regrowth within their middle exoskeletal layers, to aid normal plate enlargement. It would appear that *P. symondsi* was at least capable of using resorption and regrowth to repair broken exoskeletal components (Pl. 6, fig. 5; Text-fig. 10).

Secondary formation of tubercles overlying and replacing primary tubercles has been described in various heterostracans. These formed to repair worn or damaged regions (Tarlo and Tarlo 1965; Tarlo 1965, 1966; Denison 1973), were preceded by resorption rather than wear (Gross 1961), or represented a normal process of growth (Ørving 1976). In *P. symondsi* the large tubercles overlying smaller tubercles on the lateral edges of the branchio-cornual plates and front part of the rostrum are located on likely regions of abrasion.

Secondary tubercles forming to fill spaces between primary tubercles as a normal part of plate growth have not been described in the heterostracans. Despite this, the evidence of erupting and developing tubercles over the surface of an immature dorsal disc and branchio-cornual plate (Text-figs 2D and 6F) appears to show a ready ability to develop tubercles within the main body of the plates, as part of the general growth. It would seem to follow that this mode of growth of the superficial layer could have been accompanied by resorption and regrowth of the underlying exoskeletal layers.

Tarlo (1962) considered that the traquairaspidiiform units grew as isolated tesserae which ultimately fused with the main plates. Although no recognisable isolated tesserae have been found in the beds containing *P. symondsi*, it is conceivable that the units initially developed in Tarlo's suggested fashion, as is apparent from the posterior units on the ventral disc. In certain instances, they may not have fused with the main plates until their growth had ceased. However, evidence of non-cyclomorally arranged developing tubercles in an immature dorsal disc (see Text-fig. 2D) and the small posterior unit in an immature branchio-cornual plate (Text-fig. 6J), suggests that each unit was also capable of growth whilst attached to its neighbouring units and the main plate, thus providing a more or less unified mode of outward plate growth. This contained method of growth could have caused the basal laminated layer to fold inwards at the regions of contact between each unit and their contact with the main plate, thus leaving the internal 'constriction' impressions often observed at the edges of the units (Pl. 1, fig. 2; Pl. 3, fig. 4; Text-figs 2B and 6B). This mode of growth enabled the ontogenetic and phylogenetic development of the folded units forming the dorsal vane. This would suggest that the depressed region in the small dorsal vane (Pl. 1, fig. 3; Text-fig. 3D) may have contained recessed epithelial tissue, in which new tubercles would have formed.

As is evident from the most immature branchio-cornual plates (Pl. 3, figs 1 and 2; Text-fig. 6F-H), the longitudinal units were either isolated or not formed during early ontogeny.

All the known earlier traquairaspidiiform rostral plates (Dineley and Loeffler 1976) could be described as an antero-dorsal unit, formed mainly by cyclomorial peripheral growth, with enlarged tubercles at the anterior apex, where it folds to cover the dorsal margin of the oral cavity. However, in *P. symondsi*, there would appear to have been a new centre of cancellous and superficial layer growth within the main body of the plate, forming the 'pre-oral field'.

As Tarlo (1962) suggested, it would appear that the ventral, smooth central region achieved full size and developed an enclosing band of ornamented growth prior to its fusion with, or formation of, the ventral longitudinal units (Pl. 4, fig. 3; Text-fig. 8C). The development of the ventral smooth central region is not seen in any specimens, and its formation is open to speculation. The ventral central ornamentation on certain Canadian Pridolian traquairaspidiiforms (Dineley and Loeffler 1976) may illustrate the mode of origin. This grades from the unspecialized ventral tubercles in certain forms, to flattened and broad ventral ornamentation, which approaches the subdivided condition in the ventral smooth central region of *Rimasventeraspis*. The abraded regions in *P. symondsi* show (Text-figs 6D and 8E) broad flattened tubercles like the ventral pattern in the Canadian traquairaspidiiforms. Persistent abrasion on the ventral surface of active benthic animals might have triggered selection for a permanently smooth ventral central region. This would have greatly aided movement over the substrate, and might have evolved independently in different

lineages. The anomalous and non-abraded ornamentation of the *T. campbelli* Type 2 ventral disc may suggest a different lifestyle, and that the tubercle formation was still inherent, despite the possible ancestral formation of a smooth ventral central region.

The large size range of the phialaspidid adult plates is mainly due to the amount of outer peripheral growth. In the dorsal and ventral discs, growth ridges become more numerous as the region extends. This shows that the animals were capable of growth throughout life. The growth ridges influenced all exoskeletal levels and are seen most clearly as folds in the nasal laminated layer. By folding, the exoskeleton would have been able to have kept itself moulded to the animal, and it appears that the exoskeleton continued to grow for a time. The resulting excess of exoskeletal growth forced the growing edges of a plate downwards, then upwards at the resumption of underlying growth, to form a growth ridge. These corrugations not only mark the rhythmic growth cycles, but would also have strengthened the plates.

The range in proportions of the dorsal vanes, lateral keels, branchial openings, smooth ventral regions, and the number and size of units, appears to have had nothing to do with adult plate growth. No consistent variation can be observed in these parts, and it seems unlikely that they represent species or sexual differences.

From the most immature specimens, it is possible to estimate that *P. symondsii* developed its dermal plates when it was about one-third the length of the mature animal. This shows that an amocoete-like lifestyle was impractical, since a borrowing worm-shaped body, unimpeded by immobilizing plates of a carapace, would have been needed. Regardless of the great size range of orbital and pineal plates, the orbital and pineal openings show a small range in size. This suggests that the orbits and the pineal organ had probably reached full size at the onset of dermal plate development. Also, the posteriorly directed branchial ducts on the juvenile branchio-cornual plates suggest that a relatively large area of the thorax was free of the headshield. At this stage of development, the small animal would have needed sufficient mobility and field of vision to detect and evade predators. It is possible that it first fed upon planktonic organisms in the relative safety of shallow water, and moved into deeper water to consume larger food as it developed its armour and increased in size.

CONCLUSIONS

The morphology of *Phialaspis symondsii* and *Toombsaspis pococki* is sufficiently different from that of *Traquairaspis campbelli*, to necessitate the selection of two families, the Phialaspididae and the Traquairaspididae, within the order Traquairaspidiformes.

Internal impressions on the phialaspidid plates are interpreted as branchial musculature swathing the branchial duct in association with the visceral arches, which could have been used to facilitate jet-aided manoeuvrability to compensate for the lack of paired fins. A conspicuous notch surrounded by foramina in an anterior lateral plate of *P. symondsii* suggests the occurrence of paired olfactory ducts in association with clusters of tactile and taste sensory organs.

Dorsal and lateral swimming stabilizers and a smooth central ventral sliding plane in the Anglo-Welsh phialaspidids, suggests an active and mainly benthic lifestyle. These, their common occurrence, and the workings of the oral region in *P. symondsii*, would imply that these species were probably opportunist feeders, well able to catch and consume small benthic animals.

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PETER REX TARRANT

8 St Gregory's Close
Morville, Nr Bridgnorth
Shropshire WV16 4RL, UK

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